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THE PRODUCTS OF STARCH HYDROLYSIS AND THEIR METABOLISM[1]

BY P. V. VITTORIO, G. KROTKOV,[2] C. D. NELSON,[3] AND R. G. S. BIDWELL

Abstract

C^{14} labelled tobacco leaf starch digested with 1 *N* H_2SO_4 in a boiling water bath was not completely hydrolyzed to glucose even after 24 hr. After three hours' hydrolysis, paper partition chromatography with butanol–ethanol–water solvent revealed that besides glucose there were four C^{14} labelled products with R_F values lower than glucose. When these bands were fed individually to tobacco leaves in light they were incorporated into sucrose, glucose, fructose, and starch, and were better starch formers than glucose, glucose-1-phosphate, or maltose.

Introduction

Tobacco leaves which have been carrying on photosynthesis have a very high starch content and so have been used extensively for the biosynthesis of radioactive starch from $C^{14}O_2$. Since radioactive glucose has so many uses in metabolic tracer studies it is often very desirable to hydrolyze the radioactive starch in order to obtain labelled glucose. However, the authors noted that digestion of radioactive starch with 1 *N* HCl or H_2SO_4 never gave complete hydrolysis even though it was carried out in a boiling water bath for periods up to 12 hr.

It therefore appeared desirable to study the acid hydrolysis of tobacco leaf starch and the metabolism of the incompletely hydrolyzed starch fragments which were isolated by paper chromatography.

Acid Hydrolysis of Starch

The starch was prepared as described by Vittorio (2). Tobacco leaves were placed in a photosynthetic chamber in light in the presence of 5% $C^{14}O_2$. They were permitted to carry on photosynthesis for 24 hr., then killed and extracted with boiling 80% ethanol. The leaf residue was dried in a vacuum oven at 45° C., ground to a fine powder, and extracted with 52% perchloric acid. The extract was treated with 20% NaCl solution and the starch was

[1]*Manuscript received October 25, 1955.*
Contribution from the Defence Research Board, Kingston Laboratory, Kingston, Ontario.

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[The January number of this Journal (Can. J. Botany, 34 : 1-207. 1956) was issued January 24, 1956.]

precipitated with iodine as a starch iodine complex. This was washed with alcoholic sodium chloride and the complex was then broken with alcoholic sodium hydroxide. The starch was washed with alcoholic sodium chloride, further purified by precipitation with ethanol, and then dissolved in distilled water. It was hydrolyzed in a boiling water bath with 1 *N* H_2SO_4 for three hours, neutralized with dry barium carbonate, and passed through ion exchange resin columns containing amberlite IR 100 and Duolite A4. The deionized solution was then concentrated *in vacuo*, streaked on a paper chromatogram, and run in butanol–ethanol–water (52.5 : 32 : 15.5) solvent. Radioautography revealed that, besides glucose, there were four other radioactive bands as shown in Fig. 1. It therefore appeared that three hours' acid hydrolysis was not sufficient to hydrolyze the starch completely. In order to determine the time required for complete hydrolysis of starch it was decided to carry out hydrolysis for several hours and to remove samples at various time intervals. These were chromatogrammed on No. 3 Whatman paper using a butanol–pyridine–water solvent (10 : 3 : 3).

Fig. 2 shows the results obtained at different time intervals. The radioactive areas have been numbered as shown and for convenience will be referred to as bands. After 15 min. hydrolysis the bulk of the radioactivity was still in the origin area, designated band I, and the total radioactivity in band II > band III > band IV > glucose. In 30 min. band I still contained the bulk of the activity and the order of activity in the other bands was still the same although all of them contained more radioactivity. In 60 min. band I still contained a great deal of activity but bands II, III, and IV and glucose all contained much more activity than at 30 min. In 180 min. the order of activity was reversed with glucose having the greatest amount of activity. It is interesting to note that a new band which we have designated IIIA appeared for the first time. As time went on bands II, III, and IV became weaker and almost entirely disappeared. However, band IIIA still was present after 750 min.

The over-all picture of the progress of hydrolysis appears to be as follows. The origin area starts out with the highest total activity and steadily declines. Bands II, III, and IV start out with low activity values, build up to a peak in 60 min., and then with time decline to almost zero. Band IIIA appears sometime between 60 and 180 min. and declines more slowly than bands II, III, or IV. The glucose starts out with a very low value but increases steadily. It therefore appears that with the passage of time the origin area material is hydrolyzed first to band II material, which is then hydrolyzed to band III, and band III in turn is hydrolyzed to band IV which finally yields glucose. It is difficult to determine from this experiment just what is the role of band IIIA since band IV and glucose appear before band IIIA. Band IV appears to be easier to hydrolyze completely than bands II, III, or IIIA. After 750 min. hydrolysis there is still some material left at the origin which appears to be very resistant to acid hydrolysis.

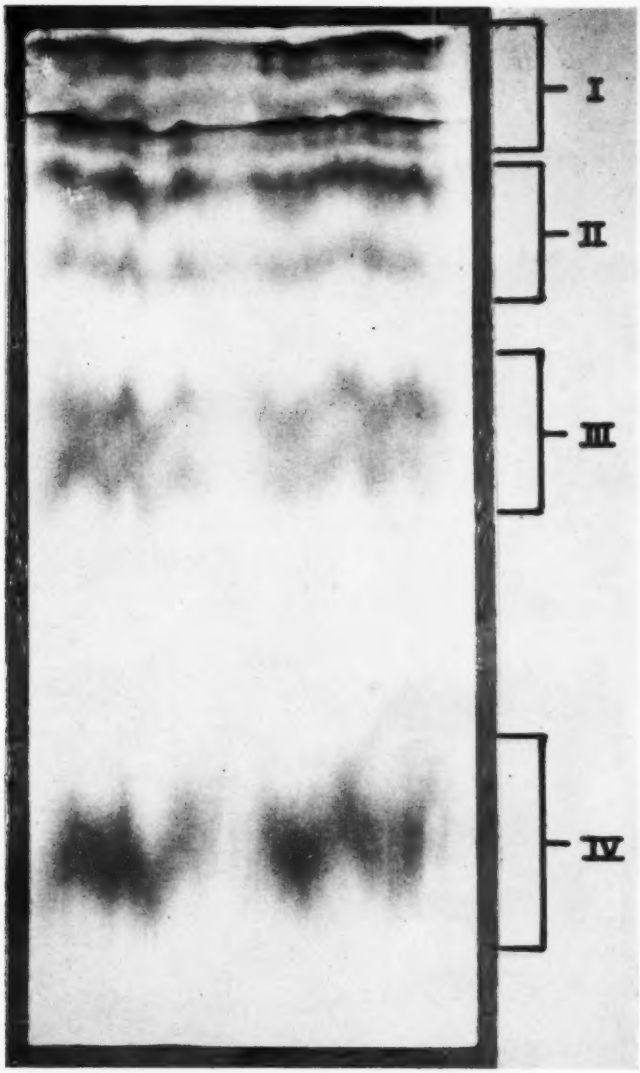

FIG. 1. Radioautogram showing four main bands from starch hydrolysis with 1 *N* H_2SO_4. The glucose band ran ahead of band IV and is not shown. Some of the bands appear to be double, but this is due to the heavy concentration of material on the origin.

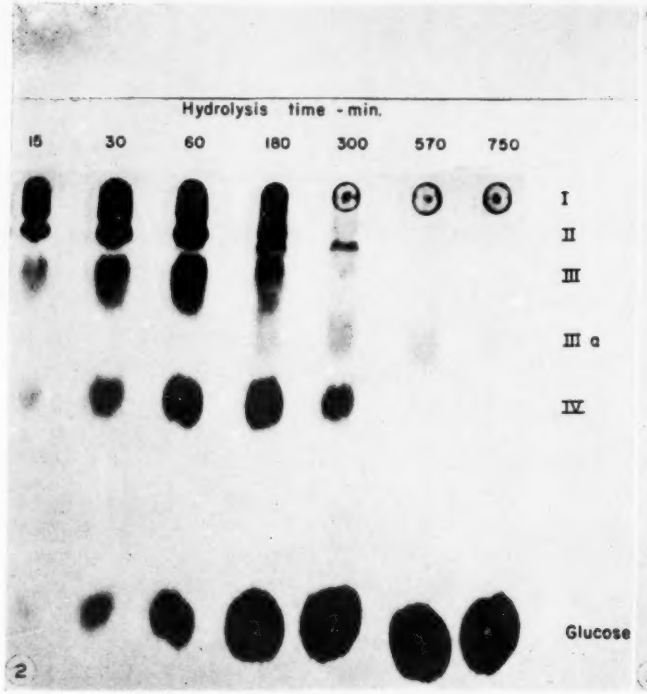

FIG. 2. Radioautogram showing the effect of 1 *N* H_2SO_4 hydrolysis on starch extracted with perchloric acid.

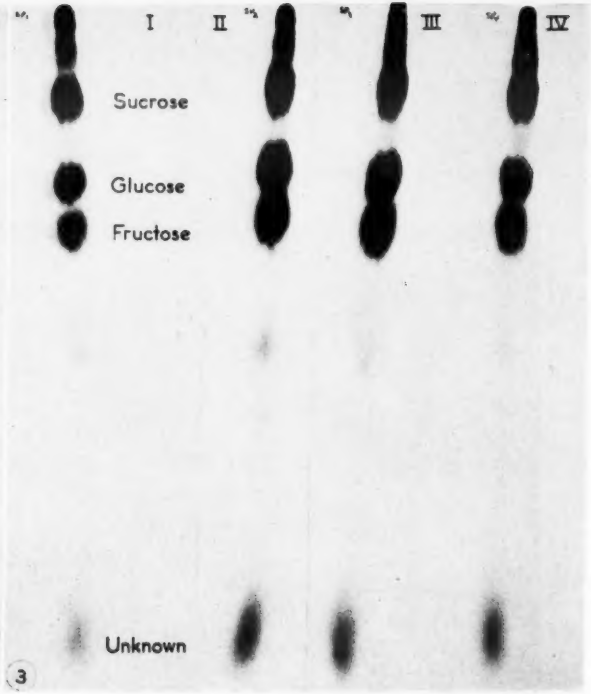

FIG. 3. Radioautograms showing the incorporation of Bands, I, II, III, and IV into the sugars of tobacco leaves.

TABLE I

THE INCORPORATION OF CARBON-14 INTO THE SUGARS AND STARCH OF TOBACCO LEAVES FED RADIOACTIVE PRODUCTS OF THE ACID HYDROLYSIS OF STARCH. VALUES EXPRESSED IN COUNTS PER MINUTE $\times 10^{-5}$

Band fed	Alcoholic extract	Origin area	Sucrose	Glucose	Fructose	Unknown cpd.	Starch	Total activity in alc. extr. + starch
1	333	130	79	27	14	5	31	364
2	406	88	130	76	55	14	81	487
3	395	53	150	66	51	17	73	468
4	406	41	140	100	54	17	66	472
1	As % of total activity in alcoholic extract plus starch	35.7	21.7	7.4	3.8	1.3	8.5	100
2		18.0	26.6	15.6	11.2	2.8	16.6	100
3		11.3	32.0	14.1	10.8	3.6	15.5	100
4		8.6	29.6	21.1	11.4	3.6	13.9	100

The question arises as to whether some of the material in the four bands in Fig. 1 might be due to recombination of glucose units during the acid hydrolysis of the starch. In order to test this, cold tobacco leaf starch (120 mgm.) was hydrolyzed in the usual manner with 1 N H_2SO_4 in the presence of 2 mgm. of C^{14} glucose containing 0.2 millicuries. At various time intervals, ranging from 15 min. to 24 hr., samples were removed, deionized, chromatogrammed, and radioautographed. In all the samples glucose was found to be the only radioactive compound. From these results one can conclude that the glucose did not combine with itself or with the products of starch hydrolysis during the acid hydrolysis of the starch.

Metabolism of the Products of Starch Hydrolysis

It may be seen from Fig. 1 that after three hours of hydrolysis four radioactive bands with R_F values lower than glucose were present on the chromatograms. It was decided to carry out an experiment to determine if they could be metabolized by tobacco leaves.

Each band shown in Fig. 1 was cut out, eluted and fed to comparable tobacco leaves in light for three hours as described elsewhere (4). The leaves were then killed and extracted with boiling 80% ethanol. The total radioactivity in the alcoholic extract was determined. The sugars in the alcoholic extract were separated by one-dimensional paper chromatography using butanol–ethanol–water solvent, followed by radioautography with "no-screen" X-ray film to locate the radioactive sugars. The resulting radioautograms for each of the fed bands I, II, III, and IV are shown in Fig. 3. The sucrose, glucose, and fructose areas were cut out, eluted, and the total activity in each was determined. The radioactive area near the origin and an unknown with an R_F higher than glucose or fructose were treated in the same manner.

The results are shown in Table I. When band I was fed, the order of total radioactivity observed in various isolated fractions was origin area > sucrose > starch > glucose > fructose > the unknown compound. For band II the order of total radioactivity was sucrose > origin area > starch > fructose > the unknown compound. When band III was fed the order of total radioactivity was sucrose > starch > glucose > origin area > fructose > the unknown compound. Band IV had sucrose > glucose > starch > fructose > origin area > unknown compound. From Table I we can see that the percentage activity in the origin area goes down as we go from band I to band IV. Since unused bands I, II, III, or IV would all be in the origin area it appears from this column that band I is metabolized the least and band IV the best. In every case more activity goes into sucrose than any other sugar or starch. In previous work (3) it was found that when $C^{14}O_2$ was fed to tobacco leaves in light the glucose and fructose contained about the same amount of radioactivity. However, in this experiment the free glucose always contained more radioactivity than fructose. One possible explanation is that the extra glucose comes from the direct hydrolysis of the fed band.

It has been observed that when C^{14} glucose, glucose-1-phosphate (4), or maltose (1) were fed to tobacco leaves in light in air there was very little (less than 2%) radioactivity incorporated into starch even though there was considerable starch synthesis. On the other hand, in the present experiments bands I, II, III, and IV all were incorporated into starch and in nearly every case starch ranked second only to sucrose in the total amount of activity incorporated from the fed band. Therefore the compounds formed during starch hydrolysis with 1 *N* H_2SO_4 are better starch formers than glucose, glucose-1-phosphate, or maltose.

Acknowledgment

The authors gratefully acknowledge the technical assistance of Miss M. J. Johnston.

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PHOTOSYNTHETIC INDUCTION IN MARINE ALGAE[1]

By K. A. Clendenning[2] and F. T. Haxo[3]

Abstract

Effects of dark time and of oxygen supply upon photosynthetic induction in *Ulva* were investigated polarographically and manometrically. Under continuously aerobic conditions, the induction period was of about two minutes' duration following one day in darkness in flowing sea water; beyond 10 min., length of the aerobic dark period had little effect. The induction period was lengthened by dark anaerobiosis, but was not eliminated entirely by dark aeration or oxygenation treatments. Aerobic induction periods of similarly brief duration were observed in *Ulva*, *Gigartina*, and *Gelidium* fronds which corresponded with those established previously for leaves and unicellular algae. Aerobic induction is attributed to an initial lack of "CO_2-acceptor" which is regenerated photosynthetically. Interpretations are provided for the widely different induction periods and saturating carbon dioxide concentrations which had been observed in earlier studies of photosynthesis in attached marine algae.

Introduction

The apparent duration of aerobic induction periods in attached marine algae has varied greatly in studies of their photosynthesis (4, 11, 19, 23). In the earliest study of photosynthetic induction, Osterhout and Haas (19) observed that photosynthesis in *Ulva* underwent a large and progressive increase during the first hour of saturating illumination, after which it proceeded at a uniform rate. Their photosynthesis measurements were based on an indicator method for dissolved carbon dioxide, and were preceded by overnight dark treatments in flowing sea water. Equally lengthy induction periods were observed under similar conditions in *Enteromorpha*, *Hydrodictyon*, and *Spirogyra*, and in *Potamogeton* leaves (19). Blinks and Skow (4) observed induction periods of "many minutes" duration when *Ulva* was subjected to overnight anaerobic dark treatments. The induction periods otherwise were of less than two minutes' duration when samples of *Ulva* fronds and *Potamogeton* and *Ricinus* leaves were examined by the platinum electrode method for dissolved oxygen (4). Blinks and Skow concluded that photosynthetic induction is probably caused by oxygen deficiency in the preceding dark period: "An induction period is . . . . absent even after rather long dark periods, provided the plant has been kept well aerated." Tseng and Sweeney (23) observed long induction periods (20–30 min.) in the red alga *Gelidium* by the Winkler method for dissolved oxygen. The respiratory absorption of oxygen and R.Q. values which Tseng and Sweeney observed in their darkened "control" samples showed that aerobic conditions

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Contribution from the Charles F. Kettering Foundation, Yellow Springs, Ohio; the Scripps Institution of Oceanography, University of California, La Jolla, Calif., New Series No. 833, and the Marine Biological Laboratory, Woods Hole, Mass.
[2]*Research Biochemist, Charles F. Kettering Foundation, Yellow Springs, Ohio.*
[3]*Chairman, Division of Marine Botany, Scripps Institution of Oceanography, University of California, La Jolla, Calif.*

were provided during their photosynthesis measurements. Emerson and Green's manometric studies of the red alga *Gigartina* (11) were made on small samples of low respiratory activity suspended in sea water which was shaken almost continuously under air (natural sea water under air, and under 5% CO_2 in air; artificial sea water under 5% CO_2 in air, and bicarbonate-buffered artificial sea water under air). The full rate of photosynthesis was observed after from 15 to 40 min. of saturating illumination in these media.

The measurement of photosynthesis in marine algae introduces special problems. Natural sea water usually contains *ca.* 3.5% dissolved salts, 2.0×10^{-3} *M* bicarbonate, and about 1×10^{-5} *M* dissolved carbon dioxide (22). The pH varies from 7.5 to 8.4 under natural conditions (22) but is usually in the range 7.8–8.1. The magnesium and calcium carbonate contents are close to saturation (22), and carbonate precipitation is promoted by the addition of bicarbonate and by the photosynthetic removal of carbon dioxide. Photosynthesis in the ocean is not limited by the natural supply of carbon dioxide (22), but the amount of plants per unit of volume is infinitely smaller ($< 10^{-6}$) than in mass *Chlorella* cultures or in the algal suspensions ordinarily used in photosynthesis research. (Strain (21) concluded on the basis of chlorophyll analyses that there are scarcely enough algae in the oceans to form a compact surface layer one cell deep.) When the algal density is increased for laboratory studies, larger reservoirs of carbon dioxide are required. If the sea water is supplemented with minimal amounts of carbon dioxide or bicarbonate, the system is weakly buffered so that large changes in CO_2 concentration and pH occur during photosynthesis measurements. If sea water is equilibrated with 5% CO_2 in air, as in two-vessel manometry, the algae are exposed to more than 100 times greater carbon dioxide and hydrogen ion concentrations than those of the natural environment. (Photosynthesis in *Gelidium* was reduced *ca.* 30% by six hours' immersion in sea water having a pH of 6.7 (23).) If concentrated bicarbonate buffers are added, magnesium and calcium carbonates are precipitated progressively, with attending pH changes. Bicarbonate buffers cannot be used as simple aqueous solutions, as with *Chlorella*; their use in monovalent chloride solutions isotonic with sea water has been discouraged by the detrimental effects of such solutions on marine algae (3).

A suitable medium for laboratory measurements of photosynthesis in marine algae would be isotonic with natural sea water and would contain calcium and magnesium for purposes of "salt antagonism" (3), but in sufficiently reduced amounts for bicarbonate buffering at any required molarity and pH. As one part of this study, the calcium and magnesium contents of natural and artificial sea water were reduced so that bicarbonate buffers could be employed at any desired strength. The effects of substituting artificial sea water, modified in this way, for natural sea water, and the effects of bicarbonate molarity at constant pH upon steady-state photosynthesis in *Ulva* were determined. Modified polarographic and manometric methods were devised with which photosynthetic induction periods of equal duration were observed

in parallel applications to samples from a single frond. The original experiments of Osterhout and Haas (19) were repeated on *Ulva* collected in the same locality, and the effects of dark treatments and of oxygen supply upon photosynthetic induction were established polarographically and manometrically. Induction in *Gelidium* (23) and *Gigartina* (11) was also re-examined.

Materials and Methods

Algae

Vegetative fronds of *Ulva lactuca* var. *rigida* (15) (or *U. rigida* (19)), collected near Woods Hole, Mass., were maintained in flowing sea water for up to two days before use in the research on methods. Disks were freshly cut from adjoining parts of the same frond in the methods' studies, and disks of unimpaired activity also were tested successively in different media. Representative samples had a fresh weight of 9.7 mgm./cm.^{2}, dry weight 2.3 mgm./cm.^{2}, and a chlorophyll content of 1.7 mgm./dm.^{2}. The fronds employed in studies of induction were selected from collections made shortly before each experiment. *Gelidium pulchrum* and *Gigartina armata* were collected near La Jolla, Calif.

Sea Water Media

Emerson and Green (11) suggested that the calcium and magnesium contents of artificial sea water might be reduced without unfavorable effects in short-term experiments, thus enabling the use of concentrated bicarbonate buffers. We have explored this possibility, using artificial sea water with the same basic formula as was employed by these workers. Upon reducing the calcium and magnesium contents to one-fourth, while maintaining the ionic strength with extra sodium or potassium chloride, carbonate precipitation did not occur in the presence of 0.025 *M* bicarbonate buffers. The concentration of dissolved carbon dioxide provided by bicarbonate buffers is increased by the sea water salts, and our studies have shown that it is seldom necessary to employ a bicarbonate concentration above 0.025 *M*. When the calcium and magnesium contents were reduced to 1/10th, 0.1 *M* bicarbonate buffers could then be employed*; the artificial sea water used in the calibration studies reported below contained only 1/10th the usual amount of calcium and magnesium.

Natural sea water was used in comparative studies of media without modification as well as after it was decarbonated by boiling with hydrochloric acid (20% vol. loss, pH 4.5): the cooled solution was adjusted to pH 7.0 with carbonate-free sodium hydroxide and diluted to original volume. Such solutions retain trace elements of natural sea water. In contrast, the artificial sea water was employed without supplementary trace elements.

* *Artificial sea water of reduced calcium and magnesium content has also been successfully used in photosynthesis measurements on the halophytic red alga Porphyridium cruentum, and on a wide variety of green, brown, and red marine algae (F. T. Haxo, unpublished), as well as in studies of the marine dinoflagellate Gonyaulax (16).*

Natural sea water may be used with quite concentrated bicarbonate buffers if part of the calcium and magnesium is removed beforehand with carbonate. Using sea water obtained at Woods Hole, Mass., and Miami, Fla., treatment with 0.025 *M* and 0.05 *M* Na_2CO_3 (solid) removed sufficient calcium and magnesium to allow the decarbonated filtrate to be employed with 0.015 *M* and 0.025 *M* bicarbonate buffers respectively at pH 8.5. Alternatively, residual carbonate in the clear filtrate may be used as the source of carbon dioxide by adjustment of the pH downward to 8.5 before use. These treatments involve small salinity changes which could be corrected by volume adjustment.

Carbon Dioxide Concentration

Dissolved carbon dioxide in bicarbonate-buffered artificial sea water (Table I) was calculated with Buch's dissociation constants for bicarbonate/carbonate in sea water at 25° C., chlorinity 19 : $pK_{Cl} = 5.939$ (9); $pK'_2 = 8.95$ (8). Buch (8) has shown that the same dissociation constants may be used in estimating carbon dioxide concentrations in artificial and natural sea water of the same salinity.

The Platinum Electrode Method

In earlier applications, thallus strips were pressed against a flat platinum electrode either with a thin disk of agar (4) or with a band of cellophane which was tightened with a winding rod (14). Fruiting margins of *Ulva* thallus have a high respiration rate, and they exhibited lengthy "anaerobic-type" induction periods when examined by the platinum electrode method (15). For the present studies, this method was modified so that one side of

TABLE I

CARBON DIOXIDE CONCENTRATIONS IN BICARBONATE-BUFFERED ARTIFICIAL SEA WATER (CHLORINITY 19, 25° C., $pK'_2 = 8.95$, $pK_{Cl} = 5.939$)

	Bicarbonate–carbonate molarity		
	0.015 *M*	0.025 *M*	0.05 *M*
pH	Dissolved CO_2, moles/liter $\times 10^{-5}$		
7.7	24.6	41.0	82.1
7.8	19.3	32.1	64.2
7.9	15.1	25.1	50.2
8.0	11.7	19.5	39.0
8.1	9.44	15.6	30.2
8.2	6.98	11.6	23.3
8.3	5.34	8.87	17.8
8.4	4.04	6.73	13.5
8.5	3.04	5.07	10.1
8.6	2.26	3.77	7.54
8.7	1.66	2.77	5.54
8.8	1.21	2.01	4.03
8.9	0.86	1.44	2.88
9.0	0.61	1.03	2.05

the thallus was in as close contact with the electrode as before, but with the other side in immediate contact with agitated sea water. The ends of thallus strips were rolled over aluminum foil and sewn to adjustable supports with which the thallus was drawn firmly against the electrode for photosynthesis measurements. During lengthy dark treatments, the thallus was released so that both its surfaces were bathed with agitated sea water. Oxygen consumption by the electrode in darkness was minimized by turning off the polarizing current except for a few minutes prior to illumination (saturating white light, *ca.* 25° C.). Galvanometer readings were made visually at minimum intervals of five seconds. The apparatus and conditions otherwise were similar to those used in earlier studies (14, 15). Our polarographic measurements differed from those of Blinks and Skow (4) in that we employed a higher (saturating) light intensity, a higher carbon dioxide concentration, and longer successive periods of illumination.

Manometric Methods

Warburg's method (27) involving intermittent illumination was modified for marine algae as follows: a small frond sample was placed in 5 ml. of artificial sea water containing at least 0.015 *M* bicarbonate/carbonate, pH 8.5–8.7. After dark equilibration (220 r.p.m., 1.6 cm. stroke), the vessels were illuminated briefly with saturating white light for different lengths of time; the illumination periods were separated by 10 min. dark intervals. After each illumination, the manometers were read successively at one minute intervals until the full yield of oxygen was observed. This method was useful in reference applications, but was unsuitable for use with lengthy dark periods.

A few measurements of photosynthesis in *Ulva* were made by the two-vessel method. Matched disks were placed in 7 ml. artificial or natural sea water contained in rectangular vessels of unequal volume. The vessels were gassed with 5% CO_2 in air, equilibrated in darkness, then illuminated with saturating light for two hours. The gas solubilities used in the two-vessel equations were $\alpha^{25°}_{CO_2} = 0.68$, $\alpha^{25°}_{O_2} = 0.022$ (22).

Direct measurements of photosynthetic capacity were made under conditions physically similar to those employed by Emerson and Green (11). A small thallus disk (1.8 cm.^{2}) was placed in a rectangular vessel with 7 ml. artificial sea water of reduced calcium and magnesium content, containing at least 0.015 *M* bicarbonate. Oxygen evolution under an atmosphere of air was determined by simple manometry at pH 8.4–8.7. For direct manometric measurements of the initial time course, the thallus area was increased, the liquid volume and vessel size was reduced, and the vessels were shaken at high speed. Narrow rings of filter paper were placed around the outer and inner edges of the main compartment of a conical vessel having a center well and venting sidearm. An annular ring of thallus, area 6 cm.^{2}, was blotted and placed on the bottom of the vessel, between the rings of filter paper. From 1 to 2 ml. of bicarbonate-buffered artificial sea water, initial pH 8.5–8.6,

was placed on the thallus, and a further milliliter was placed in the sidearm. The vessel was shaken (180 2-cm. oscillations/min.) so that a ripple of sea water crossed the thallus six times each second. The liquid in contact with the thallus remained in equilibrium with that which was held loosely in the filter paper. After dark equilibration, the thallus was illuminated with saturating white light.* The time course of photosynthesis was followed at one minute intervals, and the extra milliliter of sea water was tipped in after a steady rate of photosynthesis was attained. Manometric response was very rapid and carbon dioxide exchange could be neglected under these conditions.

Results

Photosynthesis in Bicarbonate-buffered Sea Water

In selecting a medium for use in direct manometric measurements, it was necessary to determine the effect of substituting artificial for natural sea water, and to establish the bicarbonate molarity, pH, and CO_2 requirements.

When 1.8 cm.^{2} *Ulva* disks were illuminated in 7 ml. natural sea water, initial pH 7.9, the pressure increments rose during the first 20 min., after which they remained relatively constant for 40 min. The pH rose from 7.9 to 8.4–8.5 during one hour of saturating illumination, which would be associated with a decrease in the carbon dioxide concentration from *ca.* 12 to 3×10^{-6} *M*. The observed net rate of photosynthesis during the second and third 20 min. periods was 20–25 mm.^{3} O_2/hr./cm.^{2}, using fresh as well as recently boiled sea water. Upon incorporating 0.015 *M* $KHCO_3$ – 0.001 *M* Na_2CO_3 ("E" buffer (11)) in decarbonated sea water, the corresponding rate of photosynthesis ($H \cdot K_{O_2}$ for 20–60 min.) was 43–46 mm.^{3} O_2/hr./cm.^{2} in samples from the same frond. Upon incorporating "E" buffer in artificial sea water containing 1/10th calcium and magnesium, the rate of photosynthesis was again 43–46 mm.^{3} O_2/hr./cm.^{2} (duplicate measurements). Two-vessel measurements in artificial sea water under 5% CO_2 showed 39.3 mm.^{3} O_2 evolved and 39.8 mm.^{3} CO_2 absorbed per hour per cm.^{2}, again using disks from the same frond. A repetition of the above experiment on freshly harvested *Ulva* revealed approximately equal rates of photosynthesis in natural sea water under 5% CO_2, in decarbonated sea water plus "E" buffer, and in artificial sea water plus "E" buffer (55–60 mm.^{3} O_2/hr./cm.^{2}). When the initial pH of the artificial sea water was adjusted to 8.65, the rate of photosynthesis during the first hour remained the same as under 5% CO_2 in air. Artificial sea water thus could be substituted for natural sea water in experiments involving up to two hours immersion, and a saturating supply of carbon dioxide was provided by Emerson and Green's "E" buffer at an initial pH of 8.65.

** Collimated light from a 1000 watt projection lamp was filtered through 3 in. of M/35 copper sulphate and through 18 in. of water before entering the vessel. No manometric response was detected upon illuminating heat-inactivated thallus under nitrogen with 5400 ft.-c. white light under these conditions. The saturating light requirement for Ulva at 25° C. was ca. 1500 ft.-c. under the manometric conditions. Reflection from the bright platinum electrode reduced the saturating light intensity to ca. 1000 ft.-c. under the conditions of the polarographic method.*

A pH of 8.5 was selected as the minimum at which gaseous CO_2 absorption could be neglected on the following basis. The apparent rates of oxygen production by *Ulva* ($H \cdot K_{O_2}$) were followed in pairs of vessels having different gas/liquid ratios and containing 0.015 *M* bicarbonate in artificial sea water, initial pH 7.9. As the medium became more alkaline, the pressure increments rose, and the apparent rates of oxygen production became the same in each vessel; at this stage, the minimum pH value was 8.3–8.4. The rate of photosynthesis remained unchanged as the pH rose to 8.7–8.8. The rate of photosynthesis observed with bicarbonate-buffered artificial sea water having an initial pH of 8.5 was as high as was observed under any other set of conditions.

Effects of bicarbonate concentration at an initial pH of 8.5 are shown in Table II. The rate of photosynthesis observed during the first hour did not differ significantly in the presence of 0.015–0.1 *M* bicarbonate. There was a small decline during the second hour at the lowest bicarbonate concentration, and a large decrease occurred during the third hour at all bicarbonate levels. The latter decrease must have been caused by the artificiality of the medium rather than by a limiting CO_2 supply. (Several hours immersion in artificial sea water has a detrimental effect on *Ulva* even in darkness.) For that reason, thallus samples were always maintained in natural sea water until shortly before the photosynthesis measurements were begun.

The Carbon Dioxide Requirement

Our studies indicate that the full rate of photosynthesis in *Ulva* (1.8 cm.^{2} in 7 ml.) is supported for one hour by 0.015 *M* bicarbonate, initial pH 8.5, and for two hours by 0.025 *M* bicarbonate. These media provide initial carbon dioxide concentrations of 3×10^{-5} *M* and 5×10^{-5} *M* respectively (Table I). A carbon dioxide concentration of 3×10^{-5} *M*, as provided by the former medium, similarly supported the full rate of photosynthesis in two red algae investigated, *Gelidium pulchrum* and *Gigartina armata*, i.e. 9 ml. and

TABLE II

PHOTOSYNTHETIC ACTIVITY OF *Ulva* FROND DISKS AT 25° C. IN ARTIFICIAL SEA WATER CONTAINING DIFFERENT AMOUNTS OF BICARBONATE, INITIAL pH 8.5 (mm.^{3} O_2/hr./cm.^{2})

Time	Bicarbonate molarity			
	0.015 *M*	0.025 *M*	0.05 *M*	0.10 *M*
1st hour	58	56	60	56
2nd hour	50	56	55	56
3rd hour	38	38	35	—
Final pH	9.0	8.9	8.8	8.6

6.9 ml. O_2/hr./gm. solids respectively. By contrast, much higher saturating carbon dioxide concentrations have been reported for related red algae as follows: for *Gelidium cartilagineum*, 10×10^{-5} *M* (Tseng and Sweeney (23)); for *Gigartina Harveyana*, 36×10^{-5} *M* (Emerson and Green (11)). The following considerations serve to reduce these discrepancies. As Emerson and Green pointed out, use of Buch's revised values for pK'_2 reduces their calculated carbon dioxide concentrations by 40%; with this revision, their saturating carbon dioxide concentration becomes $20–25 \times 10^{-5}$ *M*, which is still about ten times higher than we observed. The pH value is of critical importance in calculating the carbon dioxide concentration; Emerson and Green (11) used the initial pH values, and Tseng and Sweeney (23) used averages of the initial and final pH values. Weakly buffered sea water was used in both of these studies so that the pH rose and the carbon dioxide content fell during the photosynthesis measurements. Had the maximum pH value *during* steady-state photosynthesis been used in the calculations (11, 23), the saturating carbon dioxide concentration then would agree rather closely with our observations.

Photosynthetic Induction After Various Dark Treatments

A large *Ulva* frond was placed under 200 ft.-c. white light in flowing sea water immediately after harvest; a second frond from the same collection was halved; one half-frond was placed in flowing sea water, and the other was placed in a masked jar of natural sea water through which nitrogen was bubbled continuously after the jar was closed with a two-hole stopper; both half-fronds were maintained in total darkness at 20–25° C. Disks and strips of thallus tissue were cut and prepared for photosynthesis measurements in very dim light. Artificial sea water low in calcium and magnesium (1/10th) and containing 0.015 *M* $KHCO_3$, initial pH 8.5, was employed in the manometric and polarographic measurements (Figs. 1–4).

Manometric time courses of photosynthesis in *Ulva* that had been subjected in the Warburg vessels to one hour in darkness under air and nitrogen are shown in Fig. 1. A constant rate of photosynthesis was attained in the aerobic samples within two minutes (Fig. 1*a*). Upon illumination of the anaerobic samples, there was an initial "gush" followed by an induction period which regularly lasted for more than ten minutes. The time courses observed following one hour of dark anaerobiosis varied between the extremes shown in Fig. 1*b* and 1*c*; the full rate of photosynthesis was observed within 15 min. in some samples, others had not recovered completely after 30 min. illumination.

The initial changes in photosynthetic activity reported in Figs. 2 and 3 are of particular interest since they refer to *Ulva* that had been held in flowing sea water for a full day in darkness. The parallel manometric (Fig. 2) and polarographic (Fig. 3*a*) measurements revealed only brief induction periods of approximately two minutes' duration, after which photosynthesis proceeded steadily and quite as rapidly as in the "control" thallus that had been continuously illuminated in flowing sea water.

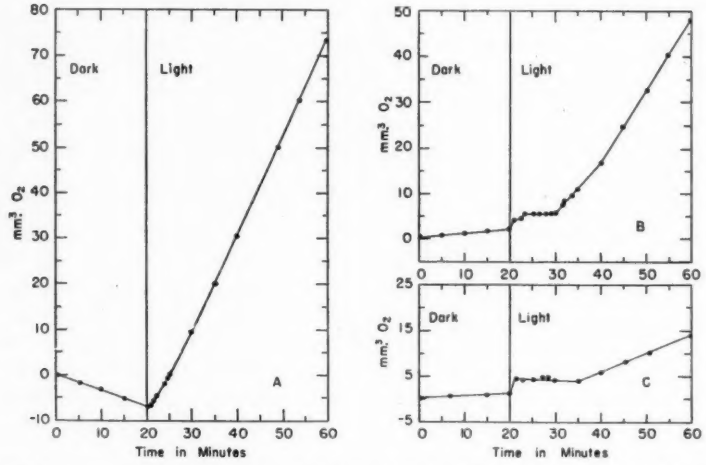

FIG. 1. Manometric time course of photosynthesis in *Ulva* after one hour in darkness (A) under an atmosphere of air, (B) and (C) under an atmosphere of nitrogen.

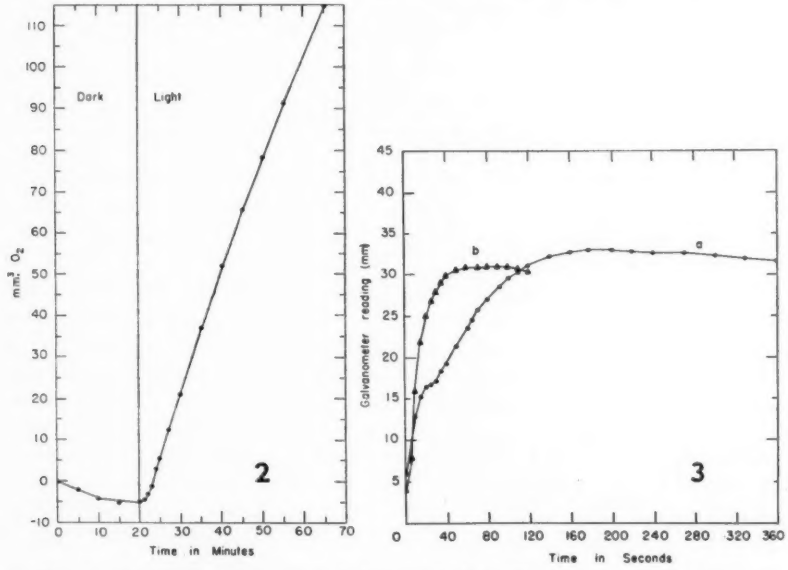

FIG. 2. Manometric time course of photosynthesis in *Ulva* after 26 hr. in darkness in flowing sea water.

FIG. 3. Initial changes in photosynthetic rate observed polarographically in *Ulva* after 26 hr. in darkness in flowing sea water (*a*) initial six-minute illumination, (*b*) second illumination following a two-minute dark interval. The time courses for subsequent illuminations (with two-minute dark intervals) closely resembled curve (*b*). The difference in time required to achieve the "steady-state" rate of oxygen production (i.e. plateau) is a measure of the induction loss after a 26 hr. vs. a two minute aerobic dark period.

Following lengthy aerobic dark pretreatments, the polarographic measurements regularly revealed a brief "oxygen gush" during the first few seconds in light (Fig. 3*a*). After the full rate of photosynthesis was attained, the thallus was subjected to a two-minute aerobic dark period, then illuminated a second time. The full rate of photosynthesis now was attained during the first minute, and the "oxygen gush" was no longer evident (Fig. 3*b*). These polarographic measurements demonstrated that lengthy aerobic dark pretreatments (up to 26 hr.) cause induction periods in *Ulva* which are not more than 90 sec. longer than following two-minute dark periods.

Manometric data for the half-frond which was held in darkness overnight under an atmosphere of nitrogen are shown in Fig. 4. One subsample was shaken for one hour in darkness under nitrogen, and a second subsample was simultaneously subjected to one hour in darkness under air. (Both were only briefly exposed to air while being transferred to the manometer vessels.) After an initial "gush", gas exchange was negligible during 40 min. illumination under nitrogen. Under an atmosphere of air, photosynthesis proceeded at a low rate after a brief initial "gush" (Fig. 4). Dark aeration of *Ulva* thallus for one hour after it had been held overnight under nitrogen thus caused a partial restoration of its capacity for photosynthesis. Hydrogen evolution apparently was responsible for the initial "gush" from anaerobic *Ulva* which was regularly observed manometrically (13).

The time courses reported in Figs. 2–4 were observed on samples from adjoining parts of a single frond in a coordinated experiment, and those reported in Fig. 1 were observed on a second frond collected at the same time. The following polarographic and manometric measurements were made independently.

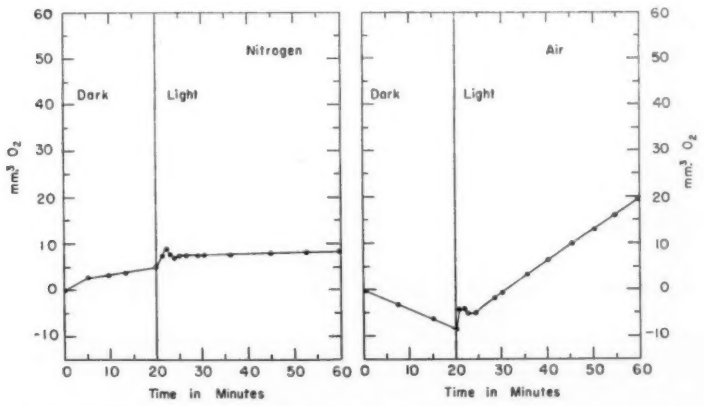

FIG. 4. Manometric time course of photosynthesis in *Ulva* after 24 hr. in darkness under an atmosphere of nitrogen; subsamples equilibrated for one hour under atmospheres of air and nitrogen.

Fig. 5 reports the initial changes in photosynthetic rate which were observed polarographically on *Ulva* that had been maintained for two hours in darkness under an atmosphere of nitrogen. (The sea water medium was gassed with nitrogen during the polarographic measurements in light and darkness.) The photosynthetic rate rose slowly during the first six minutes in light. A succession of illuminations separated by two-minute dark intervals raised the rate of oxygen production to a maximum after 15 min. illumination. Fig. 5 illustrates the marked effect of brief periods of anaerobiosis upon photosynthetic induction in *Ulva*: upon extension of the anaerobic dark interval from 2 to 10 min., the duration of the induction period was approximately doubled.

After 10 and 15 min. aerobic dark periods, the photosynthetic time courses were the same (Fig. 6) as following overnight dark treatments (Fig. 3): there was an initial oxygen "gush", a secondary peak appeared within the first minute, and the full rate of photosynthesis was attained within the second minute. After three minutes in light, the thallus was maintained in darkness for three minutes under aerobic conditions and again illuminated. The full rate of photosynthesis now was attained during the first minute. Figs. 3 and 6 demonstrate that aerobic induction in *Ulva* remains essentially the same, under the conditions of the polarographic method, upon extension of the dark treatment at room temperature from 10 min. to more than 24 hr. Fig. 7

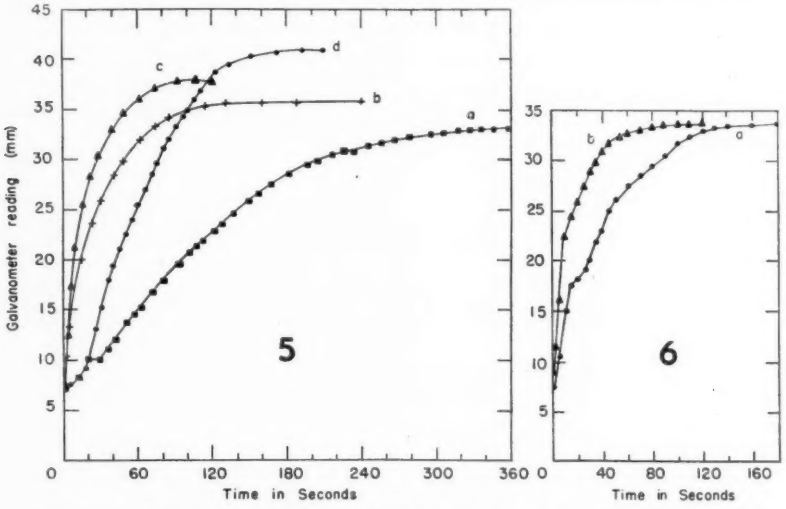

FIG. 5. Initial changes in photosynthetic rate observed polarographically in *Ulva* after two hours of dark anaerobiosis (*a*) initial six-minute illumination, (*b*) second illumination after a two-minute dark period, (*c*) third illumination after two-minute dark period, (*d*) fourth illumination after a 10-min. anaerobic dark period.

FIG. 6. Initial changes in photosynthetic rate observed polarographically in *Ulva* after 10 (or 15) min. aerobic dark periods (*a*) first illumination, (*b*) second illumination preceded by three-minute aerobic dark period.

shows that this is also true under the conditions of the manometric method: the first illumination period of Fig. 7 was preceded by a 17-hr. dark period, and the second illumination was preceded by a 20-min. dark period: the induction periods were of the same brief duration in both cases.

Photosynthetic Induction Under Pure Oxygen

Blinks and Skow (4) had indicated that photosynthetic induction in *Ulva* fronds and higher plant leaves could be entirely eliminated by thorough aeration in the preceding dark periods. Several of the accompanying figures refer to *Ulva* which was thoroughly aerated throughout the dark periods, yet brief induction periods had been observed consistently, manometrically and polarographically. Since photosynthetic induction in *Ulva* was not eliminated under our conditions by aeration, effects of pure oxygen were determined manometrically. When the thallus samples were maintained under an atmosphere of oxygen during the dark periods and during the photosynthesis measurements, the induction periods remained the same as under an atmosphere of air. This observation has been confirmed in corresponding experiments at 25° C. on two strains of *Chlorella pyrenoidosa* and on *Nostoc muscorum* (7). Experiments also were conducted in which the atmosphere of

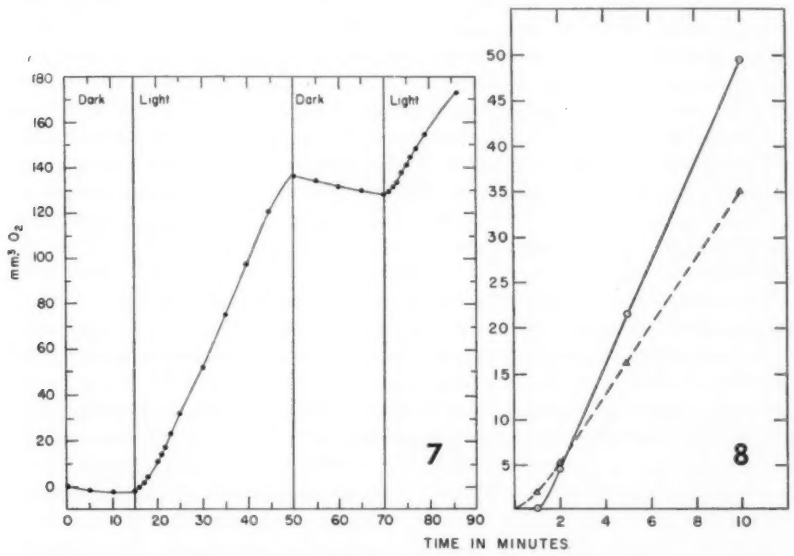

FIG. 7. Manometric time course of photosynthesis in *Ulva* after a 17 hr. aerobic dark period (first illumination) and after a 20-min. aerobic dark period (second illumination).

FIG. 8. Manometric time course of photosynthesis in *Gelidium* and *Gigartina*. Ten hour aerobic dark treatment before the first illumination (2000 ft.-c.) in artificial sea water (1/4th calcium and magnesium) 0.015 *M* $NaHCO_3$, pH 8.7, 20° C. △ - - - - - △, 270 mgm. fresh wt. of *Gigartina* (4 cm.²) ○————○, 170 mgm. fresh weight of *Gelidium*.

pure oxygen was replaced with air in darkness, 25 min. before the thallus samples were illuminated. Air was restored in these experiments to allow photosynthesis to be measured at the same oxygen tension following dark periods under air and oxygen atmospheres. In the latter experiments the induction losses ranged from 0.6–1.7 minutes of steady-state photosynthesis; those observed following dark oxygenation treatments were not significantly smaller than following 10 min. aerobic dark periods.

Photosynthetic Induction in Gelidium and Gigartina

Gelidium and *Gigartina* had exhibited lengthy induction periods in manometric (11) as well as Winkler titration measurements (23). Although satisfactory interpretations of these long induction periods were obtained in the course of our work on *Ulva*, the duration of the aerobic induction period in *Gelidium* and *Gigartina* was examined experimentally. Using our adaptation of Warburg's method, the full rate of photosynthesis was attained in both of these algae within two minutes (Fig. 8).

Discussion

The main objective of this study was to learn why such widely different induction periods had been observed in earlier studies of marine algae. For this purpose, Warburg's method involving intermittent illumination was adapted, and a direct manometric method was also devised with which induction periods of the same duration were observed as with Warburg's method and with the platinum electrode method. Our measurements of aerobic induction periods in the marine algae which were employed in earlier studies (*Ulva* (4, 19), *Gelidium* (23), *Gigartina* (11)) have shown that they do not differ appreciably from those of *Chlorella* or of higher plant leaves. In undertaking to interpret the earlier observations, it should be recalled that photosynthesis is controlled by intracellular conditions which can only be assessed indirectly.

Our studies have shown that the long induction periods observed in *Ulva* by Osterhout and Haas (19) were not caused by the overnight dark treatments in flowing sea water which preceded their photosynthesis measurements: the induction periods were found in the present study to be no longer after a full day in darkness in flowing sea water than after 10 or 20 min. aerobic dark periods; the rate of photosynthesis observed after the second minute in light also was as high as in thallus samples that had been continuously illuminated in flowing sea water. The factor or factors causing the long induction periods in the original investigations (19) must have operated after the thallus samples were transferred to the vessels used in measuring photosynthesis. Natural sea water containing alcoholic phenolphthalein was employed in the vessels (*ca.* 5×10^{-3} *M* ethanol, 3×10^{-4} *M* phenolphthalein), but Osterhout and Haas stated that photosynthesis was not affected by this internal indicator. Since the sea water was replaced periodically during the photosynthesis measurement (19) strongly limiting carbon dioxide concentrations were

avoided (6). The long induction periods observed by Osterhout and Haas (19) apparently were caused by anaerobic conditions which developed within the thallus just before it was illuminated. *Ulva* samples (10–15 cm.^{2}) were coiled within small glass cylinders, capacity *ca.* 5 ml., so that the stiff thallus lined and pressed against the inner glass surface (19). The vessel was then filled with sea water, stoppered, and shaken intermittently. The cell fluid would initially be in equilibrium with aerated sea water, which contains 5 ml. dissolved oxygen/liter at 25° C. (22). The maximum amount of oxygen within the darkened thallus can be assessed from its water content, and the frequency with which it is replaced under aerobic conditions may be calculated from the respiration rate. According to our observations, the turnover time for oxygen in *Ulva* at 25° C. in darkness is from one to two minutes. Aerobic conditions could be maintained in the Osterhout-Haas experiments if the vessel contents were kept constantly in motion. With the vessels temporarily at rest, the development of an anaerobic state would become possible. Lengthy induction periods were observed regularly by the authors in *Ulva*, polarographically and manometrically, when oxygen was withheld, but not when aerobic conditions were maintained throughout the dark period.

Tseng and Sweeney (23) used large volumes of natural sea water with small *Gelidium* samples, with and without supplementary bicarbonate and carbon dioxide, at the temperature and light intensity of the natural environment. Their data show that aerobic respiration proceeded actively in their darkened control vessels, with an R.Q. value of 1.11 ± 0.28. (Respiration was about one-eighth of photosynthesis.) The corresponding vessels in which photosynthesis was measured must have been similarly supplied with oxygen. Provision was made for the continuous mixing of the vessel contents during the photosynthesis and respiration measurements, nevertheless little photosynthesis occurred during the first 15 to 20 min. of illumination (23). The completely filled vessels were apparently at rest, however, before the measurements were begun. Upon equilibration of the vessel contents, aerobic respiration would be resumed without an induction period, whereas a long photosynthetic induction period would be shown as an aftereffect of oxygen deficiency developed under static conditions. To test this interpretation, we examined *Gelidium* under continuously aerobic conditions with Warburg's method (Fig. 8). The photosynthetic induction period was of less than two minutes duration, beyond which the rate of photosynthesis was higher than was observed by Tseng and Sweeney (23).

The experiments of Emerson and Green (11) apparently were conducted under continuously aerobic conditions. *Gigartina* has a very low respiration rate, and small samples were used in 8 ml. vol. of sea water which were shaken almost continuously under air. Nevertheless, their data regularly show induction periods lasting for 15 min. upwards, as we observed on *Ulva* under Emerson and Green's conditions. These long induction periods cannot be explained either by oxygen deficiency or by "manometric lag", although the latter can be an important contributing factor. They are best understood by

considering separately the conditions which are imposed in sea water equilibrated under 5% carbon dioxide, and in sea water weakly buffered with bicarbonate slightly above pH 7.5. Under 5% CO_2 in air, chemical equilibration with the natural bicarbonate (11) and physiological adaptation of the cells to unusual concentrations of carbon dioxide and hydrogen ion are probably causes of long induction periods (6). The lengthy induction periods observed in bicarbonate-buffered sea water having an initial pH of 7.5–8.0 are mainly artifacts caused by inadequate control of gaseous carbon dioxide exchange. Upon raising the initial pH to 8.5 in artificial sea water solutions containing at least 0.015 *M* bicarbonate, and introducing modifications to eliminate "manometric lag", the aerobic induction periods observed manometrically and polarographically are then of a similarly brief duration. When we examined *Gigartina* under continuously aerobic conditions (Fig. 8), the full rate of photosynthesis was attained within two minutes.

The aerobic induction periods which were observed with our modified manometric methods as well as polarographically corresponded closely with those published by Blinks and Skow (4). The principal point of difference concerns the complete elimination of photosynthetic induction by aeration (4). Assuming that aerobic induction is caused by an initial lack of "carbon dioxide acceptor" which is regenerated photosynthetically (10), absence of the brief aerobic induction period may be expected following any dark treatment in which the carbon dioxide acceptor is not depleted to a limiting concentration. Shiau and Franck (20) observed instances in which an aerobic induction period was lacking when dilute suspensions of young *Chlorella* cells were first illuminated. In the present study, brief aerobic induction periods were observed consistently in *Ulva* subjected to aerated sea water or to an atmosphere of pure oxygen during the dark period as well as when illuminated. Using Warburg's method involving intermittent illumination, photosynthetic induction was not eliminated in *Chlorella* or *Nostoc* when maintained continuously under an atmosphere of pure oxygen (7). Brief induction periods are regularly shown by continuously illuminated leaves and algae when the light intensity is suddenly increased from a limiting to a saturating level (12, 18). For these reasons, we are inclined to agree with Hill and Whittingham (17) that photosynthetic cells usually exhibit a brief aerobic induction period, no matter how thoroughly they have been aerated throughout the preceding dark period.

The following plants all have exhibited aerobic induction periods of a similarly brief duration at room temperature (20–25° C.):

Algae: *Chlorella* (5, 7, 17, 18, 26, 27), *Gelidium*, *Gigartina* (authors' observations), *Hormidium* (1), *Nostoc* (7), *Protococcus* (26), *Scenedesmus* (17), *Stichococcus* (1), *Ulothrix* (26), *Ulva* (4, author's observations).
Leaves: *Chenopodium* (17), *Holcum* (26), *Lamium* (17), *Nicotiana* (26), *Ricinus* (4), *Triticum* (18).
Needles: *Sciadopitys* (26).
Mosses: *Mnium* (17).

The existence of an aerobic induction period of brief but quite uniform duration within this wide variety of plants allows unified conclusions to be drawn concerning its cause. For reasons advanced previously (10), it is attributed to an initial lack of the CO_2-acceptor compound, now known to be ribulose diphosphate which is regenerated by photosynthesis (2). Certain differences between species are apparent with respect to transitory details, which are discussed by Van der Veen (24–26).

Photosynthetic cells differ in their ability to withstand long periods of dark anaerobiosis (28), so the anaerobic induction periods may be expected to vary widely between species. Since an induction period is lacking in the Hill reaction following anaerobic dark treatments of *Chlorella* and other algae, the site of anaerobic as well as aerobic induction phenomena must be in the process of carbon dioxide assimilation rather than of water photolysis and oxygen evolution.

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POOR FRUITERS AND BARRAGE MUTANTS IN GELASINOSPORA[1]

By E. Silver Dowding[2] and A. Bakerspigel[3]

Abstract

Anomalous sterility and slow fruiting occur among the following types of cultures: (1) mated homokaryotic mycelia grown from dwarf ascospores; (2) heterokaryotic mycelia grown from normal-sized ascospores; (3) hyphal-tip cultures from heterokaryotic mycelia. Such behavior may be caused by a mutant nucleus whose nutritional factors do not complement those in the nuclei of opposite mating type. Among the sterile and slow-fruiting strains were found 'barrage' mutants. They differ in texture and growth rate from wild strains. When grown in pairs, their hyphae, as they approach each other, exhibit aversion or barrage. Progeny of mated barrage strains are likewise barrage strains.

1. Introduction

Sterility and Slow Fruiting

New species of *Gelasinospora* that have been discovered recently in the United States, Germany, Holland, and Africa (1, 2, 20) have been maintained at this laboratory. Not all of them fruited readily. One produced no ascospores unless Spanish moss was added to the medium. Another, not unless the agar was enriched with calcium chloride.

Even when the fungus is cultivated upon a medium suitable for its growth and reproduction, Campbell (3) and also Seaver (24) found that 10% of the supposedly self-fertile ascospores (of *G. tetrasperma* and of *Neurospora tetrasperma*) produced sterile cultures. Campbell suggested that the heat treatment used to induce germination may have destroyed some of the spore nuclei, or alternatively that there may have been some failure in the cytological mechanism when the spores were being formed.

In our own experiments with *G. tetrasperma* which are to be described in this paper, many of the presumably self-fertile cultures, and also some of the matings between ascospores of opposite mating types, were either completely sterile or very slow fruiting. A knowledge of the incidence and cause of this poor fruiting would make the organism more valuable for biochemical–genetic study.

Barrage

Hyphae of certain strains of *Phycomycetes*, *Ascomycetes* (15), *Basidiomycetes*, and *Fungi Imperfecti*, when they come into contact on an agar plate, exhibit a zone of aversion between them. In the fruit-tree parasite *Diaporthe perniciosa* the aversion capacity is heritable (5). In tetrapolar Basidiomycetes, mutual repulsion between different homokaryotic strains with their B factor

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in common has been called Barrage (25). In *Schizophyllum commune* for example, strains *AB* and *aB* when paired form a barrage zone where they meet. This zone has been interpreted as one occupied by a synthetic heterokaryon of the constitution *ABaB*, called a 'barrage heterokaryon' (21). In *Pleurage* (*Podospora*) *anserina*, according to Ephrussi (14), Rizet found two strains S and *s*, which form barrage but no hyphal fusions when they meet. Along the zone of contact between *S* and *S*, or between *s* and *s*, when these are of opposite mating type, a single line of perithecia develops. Along the zone of contact between strains of opposite mating types, *S* and *s*, a double line of perithecia develops, leaving a barrage strip between them.

In this laboratory we have found among the slow-fruiting and sterile cultures of *Gelasinospora tetrasperma*, strains which differ in their appearance and behavior from the wild ones. Since a staling or barrage effect appears when such strains meet, they are called 'Barrage Strains'. They extend our conception of barrage.

Homokaryotic vs. Heterokaryotic Mycelia

Unless otherwise stated, the term homokaryotic will be restricted to mycelia whose nuclei are all of the same mating type; the term heterokaryotic, to mycelia whose nuclei are some of plus and some of minus mating type.

2. Material

The *Gelasinospora tetrasperma* used in this work was obtained in 1952 from Dr. J. W. Groves, Science Service, Ottawa. It had been isolated from parsnip seed in British Columbia. It differed from the original strain isolated in 1933 (11) in its long perithecial necks and its readily germinating ascospores. Cultures are available at the Provincial Laboratory of Public Health of the University of Alberta.

The fungus undergoes reduction division and in this sense possesses sexuality. However, unlike certain other fungi (19), it is not differentiated morphologically into two sexes. In fact no strains possess spermatia although all of them possess protoperithecia (Fig. 4). Both mating types are capable of reciprocally donating and receiving nuclei which, if they are of opposite mating types, may act as gametes and fuse. One of the two mating types of mycelia and its nuclei will be arbitrarily called 'plus' and the other 'minus'.

Gelasinospora tetrasperma is one of those facultatively heterothallic species that possess both fertile and sterile strains (6, 10, 11). Fertile strains produce perithecia and ascospores; sterile strains do not, unless they are appropriately mated. Fertile strains are obtained from normal-sized ascospores; sterile strains from dwarf ascospores.

Dodge (7) has shown that the haploid nuclei in the ascospores must be either plus or minus. Normally a spore-wall surrounds each plus–minus pair and forms normal-sized ascospores. Sometimes, however, the members of the pair wander apart in the ascus cytoplasm and become walled off into two separate dwarf ascospores. Dwarf ascospores are therefore either of plus or minus mating type (Fig. 1).

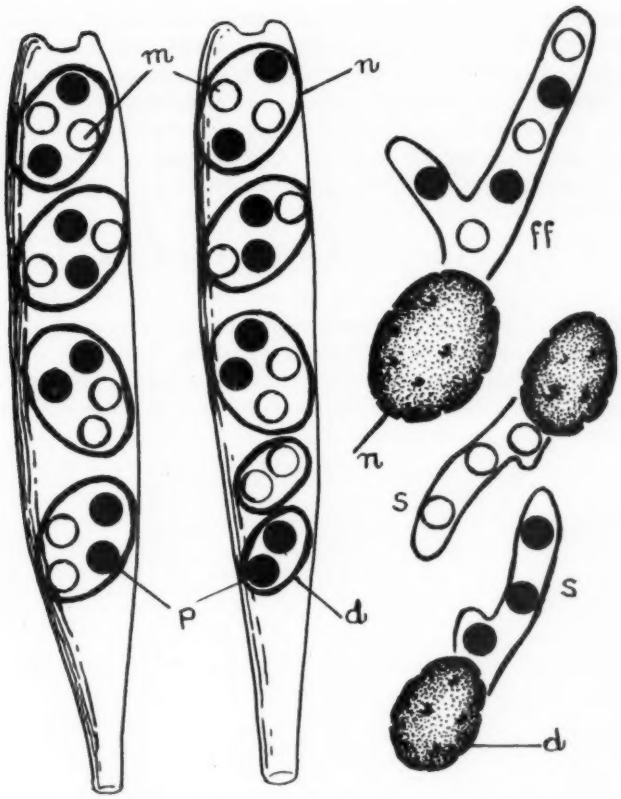


FIG. 1. Diagram of normal-sized and dwarf ascospores, some of them in asci, and some of them discharged and germinating. *n*, normal-sized spore; *d*, dwarf spore; *m*, minus nucleus; *p*, plus nucleus; *ff*, fast-fruiting heterokaryon; *s*, sterile homokaryon.

A heterokaryotic mycelium may arise directly from a single normal-sized ascospore (Fig. 1) or indirectly by fusions between two homokaryotic mycelia (13). A homokaryotic mycelium may arise from a dwarf homokaryotic ascospore (Fig. 1), from an anomalous normal-sized ascospore (3, 24), or, possibly, from an isolated hypha of a heterokaryotic mycelium (4, 9, 18, 23).

3. Methods

In making monosporous cultures, no attempt was made to secure ascospores from the same ascus or from the same perithecium. Freshly ejected ascospores were suspended in sterile water which was poured over a Petri dish of hard malt agar. The ascospores to be used, whether normal-sized or dwarf, were measured as they lay on the agar surface and their position marked with ink

on the under side of the glass dish. After 24 hr. incubation at room temperature, at least 76%, often 100% of them, would germinate. To grow a monosporous heterokaryotic culture a normal-sized germinating ascospore was transferred to a malt-agar slant. For a homokaryotic one, a dwarf ascospore was selected. To pair homokaryons, two inocula, each derived from a dwarf spore, were placed side-by-side on the same agar slant. The temperature at which all of these cultures were kept during the experiments varied between 24 and 25° C.

4. Types of Fruiting Behavior of Mated Dwarf Spores

Thirty-six dwarf ascospores were allowed to germinate in separate tubes. During the months that they were kept in culture none of them formed perithecia. The 36 homokaryons were paired in all possible combinations, and the pairings were all repeated. They were examined for perithecia after three weeks' incubation, and again at intervals during the next three months.

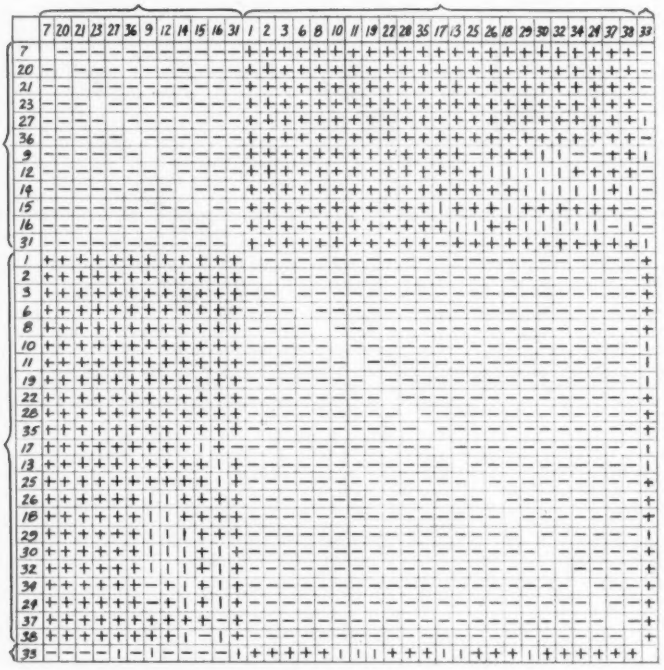


FIG. 2. Pairings made in duplicate between mycelia from 36 dwarf ascospores. The mycelia fall into two groups, plus and minus, sterile among themselves, but fertile one with the other. Among the expected fertile combinations are certain exceptions, which are either slow fruiting or sterile in one or other of the series of matings or in both: (−), sterile after three weeks in both matings; (1), perithecia formed in three weeks in only one of the matings; (+), perithecia formed in three weeks in both matings.

It can be seen from an examination of Fig. 2 that 35 of the 36 homokaryons* fall into two groups; the 12 plus strains and the 23 minus.

Six per cent of the matings between plus and minus homokaryons were either slow-fruiting or sterile. Of these, five cultures did not form perithecia until 37 days old; 14 not until 72 days. Some were still sterile even after 72 days, when they were discarded. Fig. 2 shows that a pairing between some of the plus and some of the minus strains may be slow-fruiting in the first experiment and fast-fruiting when the same pairings were made a second time. Plus homokaryon 16 was paired in duplicate with 23 minus reactors. Of the 46 total matings, 36 fruited quickly but 10 fruited late or remained sterile indefinitely.

Preliminary experiments with mated homokaryons derived from dwarf spores had previously suggested (12) that fast fruiting is dependent upon the presence of hypothetical growth factors *Ff*, and poor fruiting upon the presence of either one of them alone. However, the above experiment does not confirm the existence of such factors, because the dwarf spores can be divided into only two groups, plus and minus, and not into four.

The difference in the times required for fruiting of different pairings between the same two homokaryotic mycelia suggests variation through mutation among the hyphae of each of these two mycelia. All the nuclei of each are derived from divisions of a single haploid nucleus, yet they have come to differ one from another.

5. Types of Fruiting Behavior Among Normal-sized Spores

Types of Ascospores

One hundred and seventy-eight normal-sized ascospores were allowed to germinate separately. Each mycelium was left intact, attached to the spore from which it grew, and was never transferred to fresh media. Within 14 days 156 of the cultures behaved normally and had produced perithecia and ascospores. The remaining cultures were sterile. Twelve of these fruited, some in three weeks, some in three months, and a few even later. They might easily have been mistaken for homokaryons. The perithecia that were finally produced by the slow fruiters were small and contained few ascospores. These ascospores became fast fruiters. The remaining 10 cultures were still sterile after three months. Mating with plus and minus tester strains proved that of the 10 sterile cultures three were plus and seven were minus reactors.

Other similar experiments were carried out so that altogether the fruiting behavior of 613 normal spores was analyzed. The spores fell into four groups: (1) *fast fruiters*, producing ascospores within two weeks; (2) *slow fruiters*, producing ascospores within from three weeks to three months; (3) *plus reactors*, sterile indefinitely but fruiting after being mated with minus testers;

**Exceptional mycelium No. 33 reacted as a plus homokaryon in the second series of matings, but in the first series fruited with some of the plus homokaryons (Fig. 2). It was probably a slow-fruiting heterokaryon (see section 5).*

and (4) *minus reactors*, fruiting only with plus testers. The percentage of spores of each of the four types was: fast fruiters, 80%; slow fruiters, 10%, plus reactors, 5%; minus reactors, 5%.

Explanations for the variation in behavior among the normal-sized ascospores are suggested in section 7.

Types of Hyphae Cut from Fast Fruiters

From each of 100 normal-sized ascospores, hyphal tips 225 to 300μ long were amputated with a needle and planted separately in tubes. It is possible to arrive at a rough idea of the number of nuclei these tips contained by calculating from the previous counts of nuclei in stained *Gelasinospora* mycelia (11). A conservative estimate would be 30.

The remainder of each amputated mycelium, together with the spore from which it was growing, served as a control. These 'spore cultures' were numbered from *s* 1 to *s* 100. The hyphal-tip cultures were numbered from *t* 1 to *t* 100. Thus there were altogether 100 pairs made up of 100 '*t*' and 100 '*s*' cultures. The day after the experiment was set up it was found that there were 53 pairs of which both the *t* and the *s* cultures were growing.

Fourteen days later, all of the 53 control '*s*' cultures had fruited. Each mycelium from which the 53 hyphal tips were cut therefore must have been heterokaryotic and fast-fruiting.

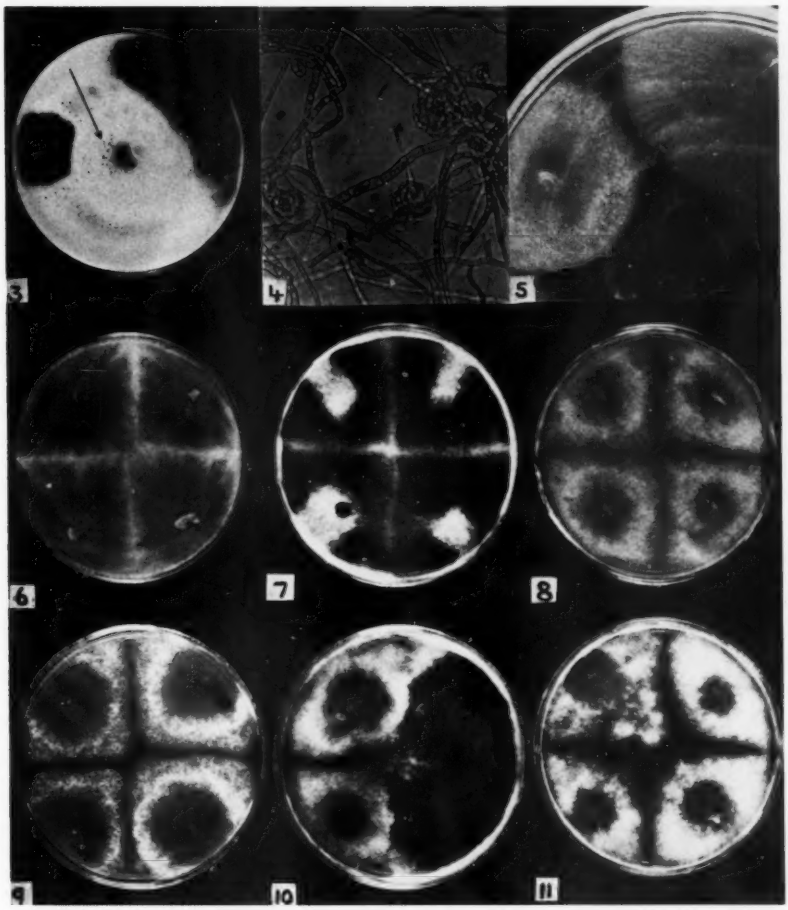
Of the 53 experimental '*t*' cultures 50 had fruited by the end of the second week. They were classified as *fast-fruiting heterokaryons*, and resembled the controls from which they had been cut. Three '*t*' cultures were sterile at this time. After the third week, one of the three sterile cultures had developed a few ripe perithecia. It was classified as a *slow fruiter*. After more than a month the remaining two cultures were still sterile and all transfers from them were sterile. Then they were both mated with plus and with minus tester races. With the plus tester they both remained sterile; with the minus they both fruited. The two cultures were classified as *plus reactors*.

From these amputation experiments we see that all fast-fruiting heterokaryons are not homogeneous. Some possess hyphal tips whose 20 or 30 nuclei are of a different make-up from the nuclei in the rest of the mycelium.

6. Barrage Mutants

Among the mycelia maintained in culture, seven were distinct in appearance and behavior, and will be known as 'barrage' strains. Six of the barrage strains were discovered among the slow fruiters and the remaining one among the minus homokaryons. None were found among the fast fruiters.

From their appearance in culture, barrage strains can be readily identified. Fig. 5 shows two slow-fruiting heterokaryotic mycelia growing side-by-side. The one to the left is a barrage strain, the other is not. As compared to the open, lax growth of the wild strains, barrage strains are matted or felted, sometimes of a yeastlike texture. Without magnification, the main hyphae of wild strains appear coarse and are readily discernible in reflected light,



FIGS. 3–11. *Gelasinospora tetrasperma*, some wild, some barrage strains, on malt agar. FIGS. 4, 9, 10, homokaryons; FIGS. 6 and 7, fast-fruiting heterokaryons; FIGS. 3, 5, 8, slow-fruiting heterokaryons. FIG. 3, explained in section 7; FIG. 4, three protoperithecia; FIG. 5, barrage strain (left) compared with a wild strain growing beside it; FIGS. 6 and 7, four inocula from the same wild strain in contact; FIGS. 8 and 9, four inocula from the same barrage strain in contact; FIG. 10, 11 days after two barrage minus strains (left) were inoculated, they were mated with two wild plus strains (right). The position of the perithecia shows the direction of nuclear migration. FIG. 11, four inocula of a barrage strain from the progeny of the mating in FIG. 10.

while those of barrage strains are too narrow to be seen. In wild strains the main hyphae usually extend beyond their lateral branches giving the colony a wavy or feathery outline. In barrage strains the main hyphae do not surpass their lateral branches so that the colony outline is smoothly circular. This particular difference is not apparent in the photograph. Finally, barrage strains grow more slowly, about half the rate of wild strains.

Dr. Wm. Carmichael, of the Provincial Laboratory of Public Health of this University, grew paired strains of *Gelasinospora tetrasperma* under special conditions for the observation of hyphal fusions (method unpublished). Whether the members of the pair were both barrage strains, both wild strains, or one wild and the other barrage, hyphae of one mycelium always fused with hyphae of the other. It is assumed that similar inter- and intra-strain fusions take place when mycelia are paired in Petri dishes in the following experiments.

A fast-fruiting monosporous culture was inoculated in four places in a Petri dish. When the mycelia met, contact between them was marked by a fluffy ridge of aerial mycelia in the shape of a cross. Twenty-three similar cultures from other spores when 'selfed' in this way also produced the same ridges (Figs. 6 and 7). Twenty-three pairings between different fast-fruiting strains behaved similarly. Wild homokaryotic strains also exhibited fluffy ridges along the contact lines.

A slow-fruiting barrage strain was then inoculated in four places in a Petri dish. The area where the mycelia met was marked by strips of apparently clear agar in the shape of a cross (Fig. 8). Although such an effect of one mycelium upon another has been known in the literature as aversion or barrage, barrage zones are not devoid of hyphae. They lack aerial hyphae but contain mycelial growth submerged in the agar. The remaining five slow-fruiting barrage strains and the one minus barrage strain were similarly tested. When selfed they produced the same type of barrage.

For some weeks, slow fruiter 19*a* had been a fast-growing, coarse-textured wild type, showing a fluffy ridge when two of its mycelia came into contact. Then two of its subcultures changed into slow-growing and fine-textured mycelia which showed barrage between them when they were paired. Similarly, minus homokaryon 13, previously of the wild type, later took on the barrage morphology and eventually showed barrage zones between paired mycelia. These two converted strains made a total of nine original barrage cultures.

Since no plus barrage strains had been discovered, they were bred by mating a minus barrage homokaryon with a plus wild homokaryon (Fig. 10). Eighty-four ascospores from this mating were germinated separately and tested for texture, for fruiting behavior, and for the formation of intra-strain barrage zones. Seventeen per cent of the heterokaryons and 20% of the homokaryons were of the barrage type.

One plus barrage strain so obtained was then mated with a minus barrage strain. From this mating all the progeny without exception were of the barrage type (Fig. 11). The ascospores isolated and tested were as follows:

eight dwarf ascospores of plus reaction; nine dwarf ascospores of minus reaction; 34 normal-sized ascospores. Each of the 51 strains showed barrage texture and intra-strain barrage, and all pairings between different strains, inter-strain barrage. Therefore, the barrage character must be heritable, and barrage strains must be mutants.

7. Explanation for Sterility and Slow Fruiting

As mentioned previously, Campbell (3) and Seaver (24) have presented two alternative explanations for the sterility among supposedly heterokaryotic ascospores. One is that the heat applied to induce germination killed either the plus or the minus spore nuclei; the other, that the mechanism ensuring that unlike nuclei are included in the same ascospore, failed. A third explanation is now offered. If during meiosis the chromatids crossed over between the centromere and the plus–minus locus, then all the spore nuclei would be of the same mating type and the spore would be sterile.

Slow fruiting cannot be explained in any of these three ways. Neither can the poor reaction between certain mated homokaryons, nor the difference in fruiting behavior between a hypha and the heterokaryotic mycelium from which it has been cut.

Mutant nuclei could explain all the phenomena here described. The number of these nuclei might determine the degree of poor fruiting in a culture. Such nuclei might be either of the following types.

(*a*) *Infrequently-dividing Nuclei*

A nucleus which divides less frequently than the other nuclei in the same spore or mycelium would upset the numerical balance of plus and minus nuclei in the cell. The existence of such a nucleus was suggested by the results of the following experiment.

Slow fruiter 19*b* was inoculated centrally on an agar plate. After the inoculum had grown over half the radius of the dish, tester homokaryons 25 (plus) and 15 (minus) were placed at the periphery opposite each other, as shown in Fig. 3. In the photograph the heterokaryon appears white and the two homokaryons almost black. It can be seen that perithecia developed on strain 19*b* nearer to the plus (left-hand) than to the minus (right-hand) tester, suggesting that strain 19*b* contains more minus nuclei than plus nuclei. However, although two or three other cultures consistently reacted like 19*b* with tester strains, other slow fruiters did not do so.

(*b*) *Nuclei Resembling in Nutritional Factors the Nuclei of Opposite Mating Type*

One would expect much variation among the nuclei within the same mycelium, especially when one considers that some of them may have migrated from other sources (12, 13). Indeed nuclei of the Fungi Imperfecti have actually been separated and have given rise to culturally distinct individuals (16, 17, 22). Nuclei of *Gelasinospora* may differ in the factors which govern the synthesis of growth substances. When the nuclei of opposite mating

type in a mycelium are similar in these factors, the fruiting behavior of a mycelium might be poor. When these nuclei contain factors that complement each other, fruiting might be vigorous (8).

In this laboratory, a mating between a wild and a barrage homokaryon of *G. tetrasperma* fruits more vigorously than a mating between two wild strains or between two barrage strains. Perithecia appear a week earlier and in greater quantities when one of the pair is a mutant and the other wild, than when both members of the mated pair are mutant or when both are wild. Such heterokaryotic vigor can be explained by the variety in the nutritional factors contributed by the two strains.

Similarity of nutritional factors in the plus and minus nuclei will explain the anomalous matings between homokaryons derived from dwarf spores, the anomalous heterokaryons derived from normal spores, and the anomalous hyphal tips amputated from heterokaryotic mycelia.

Acknowledgments

The authors are indebted to Dr. T. Johnson, Dominion Laboratory of Plant Pathology, Dr. D. W. Shaw, Faculty of Agriculture, University of Sydney, Dr. J. R. Raper, Biological Laboratories, Harvard University, and Dr. Peter Day, College of Agriculture, University of Wisconsin, for helpful discussion, and also to Mrs. W. C. Wonders of Edmonton for assistance with Fig. 2.

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STUDIES IN AMERICAN ORCHIDS. I[1]

By Leslie A. Garay[2]

Abstract

Sixteen species of tropical American orchids are described as new, and nine new combinations of taxonomic importance are proposed. These are arranged in systematic order as follows: *Xerorchis trichorhiza* (Krzl.) comb. nov.; *Sobralia kermesina* sp. nov.; *Cranichis Asplundii* sp. nov.; *Spiranthes decora* sp. nov.; *Spiranthes Wendlandiana* (Krzl.) comb. nov.; *Erythrodes Ortgiesii* (Hort.) comb. nov.; *Physosiphon Bangii* (Schltr.) comb. nov.; *Lepanthes hemirhoda* sp. nov.; *Lepanthes macrantha* sp. nov.; *Lepanthes palmaritoensis* sp. nov.; *Lepanthes pendens* sp. nov.; *Lepanthes Vareschii* sp. nov.; *Pleurothallis Killipi* sp. nov.; *Pleurothallis pachypus* (Lehm. & Krzl.) comb. nov.; *Pleurothallis Tunguraguae* var. *minor* var. nov.; *Epidendrum Cuatrecasasii* sp. nov.; *Scaphyglottis flaccida* (Krzl.) comb. nov.; *Orleanesia maculata* sp. nov.; *Polycycnis ornata* sp. nov.; *Maxillaria cuencana* nom. nov.; *Maxillaria pleuranthoides* (Schltr.) comb. nov.; *Rodriguesia Strobelii* sp. nov.; *Dipteranthus planifolius* (Rchb.f.) comb. nov.; *Telipogon ochraceus* sp. nov.; *Telipogon roseus* sp. nov.

Introduction

The increasing number of collections received by the writer from various parts of the American tropics has resulted in the recognition of many new taxa and the clarification of various previously obscure concepts. Since these taxonomic conclusions are numerous, it seems advisable to publish them in series, the first of which is presented here.

Papers of similar nature were previously published in the Arquivos do Jardim Botânico do Rio de Janeiro, Vol. 11, 12, and 13, 1951–54.

All illustrations except one were made by the writer from dried herbarium specimens, the floral details completed with the aid of camera lucida. The writer is indebted to Mr. G. C. K. Dunsterville for permission to reproduce his illustration of *Orleanesia maculata*, which he drew from living material.

The arrangement of the genera follows the phylogenetic system proposed by Dr. Rudolf Schlechter in Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem, 9: 563–591. 1926.

The writer wishes to acknowledge a grant-in-aid of research furnished by The National Research Council of Canada which made possible visits to various herbaria in the United States and the study of their collections. Sincere thanks are due to Miss Luella K. Weresub, University of Toronto, for her invaluable criticism and correction of this paper.

Description and Discussion of Species

Xerorchis trichorhiza (Krzl.) Garay, comb. nov.

Syn.: *Epidendrum trichorhizum* Krzl. *in* Fedde Rep. 25: 21. 1927.

Epidendrum trichorhizum is described from Bolivia and referred by Kraenzlin to the section "*Euepidendrum-planifolia-racemosa*" which is characterized by a terminal inflorescence and a lip fully adnate to the column.

[1]*Manuscript received December 2, 1955.*
Contribution from the Department of Botany, University of Toronto, Toronto, Ontario, Canada.
[2]*Assistant Curator of the Herbarium of Vascular Plants, University of Toronto.*

Kraenzlin's description of the species, however, states that the flowers are axillary and the lip is free from the column. An examination of an isotype (*Buchtien No. 510*!) preserved in the herbarium of the Smithsonian Institution reveals that it possesses soft, powdery pollinia, on which characteristic the tribe *Polychondreae* is based, rather than the cartilaginous pollinia of the *Kerosphaereae* to which *Epidendrum* belongs.

Epidendrum trichorhiza is therefore a member of the tribe *Polychondreae*, and undoubtedly belongs to the previously monotypic genus *Xerorchis* Schltr. originally described from the Amazon valley. A comparison with *X. amazonica* Schltr. (*Ule No. 5425*, Type!) shows that this new addition to the genus differs from the type mainly on the basis of size (being larger throughout), structure of lip (possessing two lamellae where there are none in *X. amazonica*), and surface of sepals (dorsally covered with short appressed hairs in *X. trichorhiza*, glabrous in *X. amazonica*).

A recent collection (*Oscar Haught No. 5361*!) which is referable to *X. trichorhiza* extends the distribution of this species considerably northward to Colombia, Dept. of Cauca.

Sobralia kermesina Garay, sp. nov. Fig. 10 A

Saxicola, erecta supra metrali; radicibus mihi non visis; caulibus teretibus infra a foliis destitutis, vaginis parce evanidis obtectis, supra pauci foliatis; foliis distichis, rigidis, ovato-lanceolatis, plicatis, acuminatis, basi vaginantibus, laevibus, 9–11 cm. longis, 1–2 cm. latis; inflorescentia pauciramosa; bracteis minutis, cucullato-triangularibus, ovariis pedicellatis multoties brevioribus, glabris; floribus mediocribus, kermesinis, glabris; sepalis ovato-oblongis, acutis, 5-nerviis, 3.5 cm. longis, 5 mm. latis; petalis sepalis similibus, paulo latioribus, 7-nerviis, 3.5 cm. longis, 7 mm. latis; labello obovato, antice valde bilobo, margine crenulato, disco mediano cum nervis 5 valde incrassatis a basi usque ad apicem ornato, 4.5 cm. longo, 3 cm. lato; columna gracili, angulata, apice falculis sensim evolutis donata, 2.2 cm. longa; ovariis cum pedicellis 2.5 cm. longis.

Ecuador: Río Catamayo Drainage; Hacienda Guaycopambam, on Río Guaycopamba, 20 km. south of Vilcambamba, Prov. de Loja; lat. 40°27′ S., long. 79°13′ W. Rocky open slope, lower slopes and flat bottom lands generally thorn-forest but bottom land with much ground water and broad-leafed forest. Canes erect, roots fleshy, flowers deep crimson-magenta. Alt. 1750–1800 meters (aneroid readings). Feb. 15, 1945. Coll. *F. R. Fosberg & M. A. Giler No. 23063.* Type in the author's herbarium No. 3241.

Sobralia kermesina is most closely related to *S. liliastrum* Lindl., differing from it by possession of a more elongate and branched inflorescence, much smaller bracts, smaller and differently colored flowers, a deeply bilobed lip, and an entirely different column. *Sobralia Malmquistiana* Schltr. has a very similar lip, but its flowers are three times as large as those of *S. kermesina*

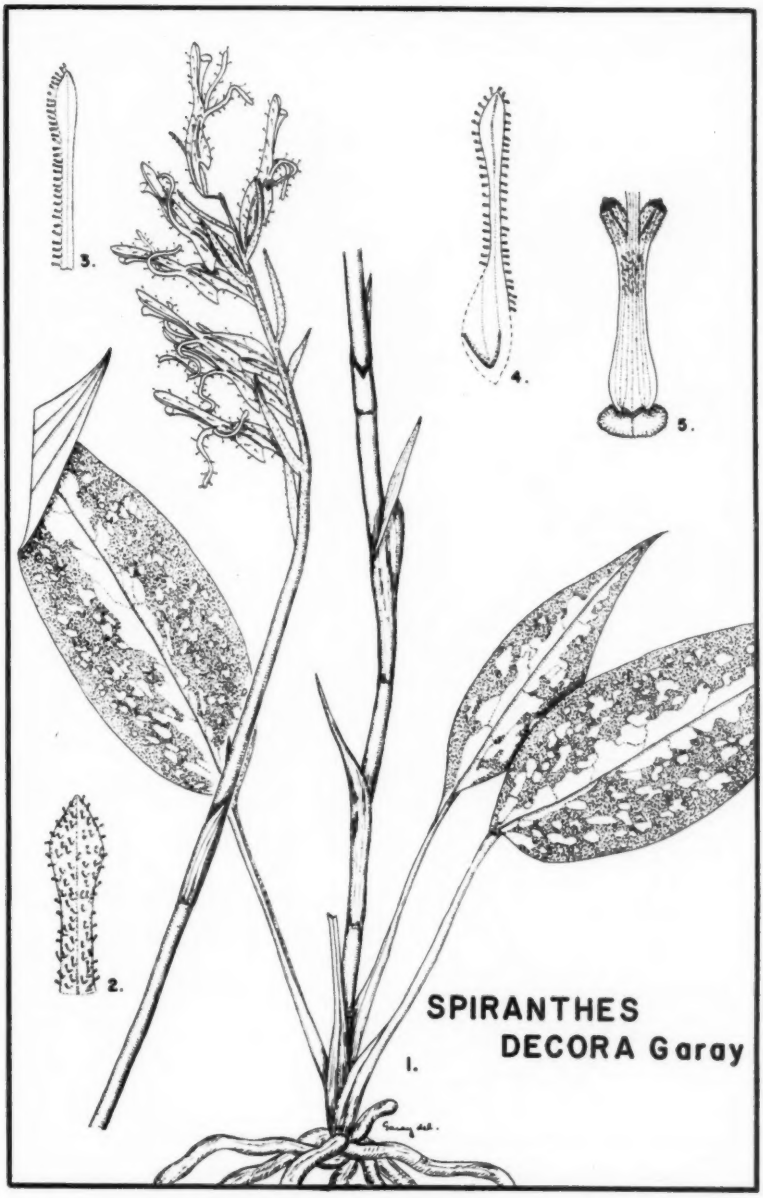


FIG. 1. General habit of plant × 2/3. FIG. 2. Dorsal sepal, back view × 1.5. FIG. 3. Petal × 1.5. FIG. 4. Lateral sepal × 1.5. FIG. 5. Lip × 1.5.

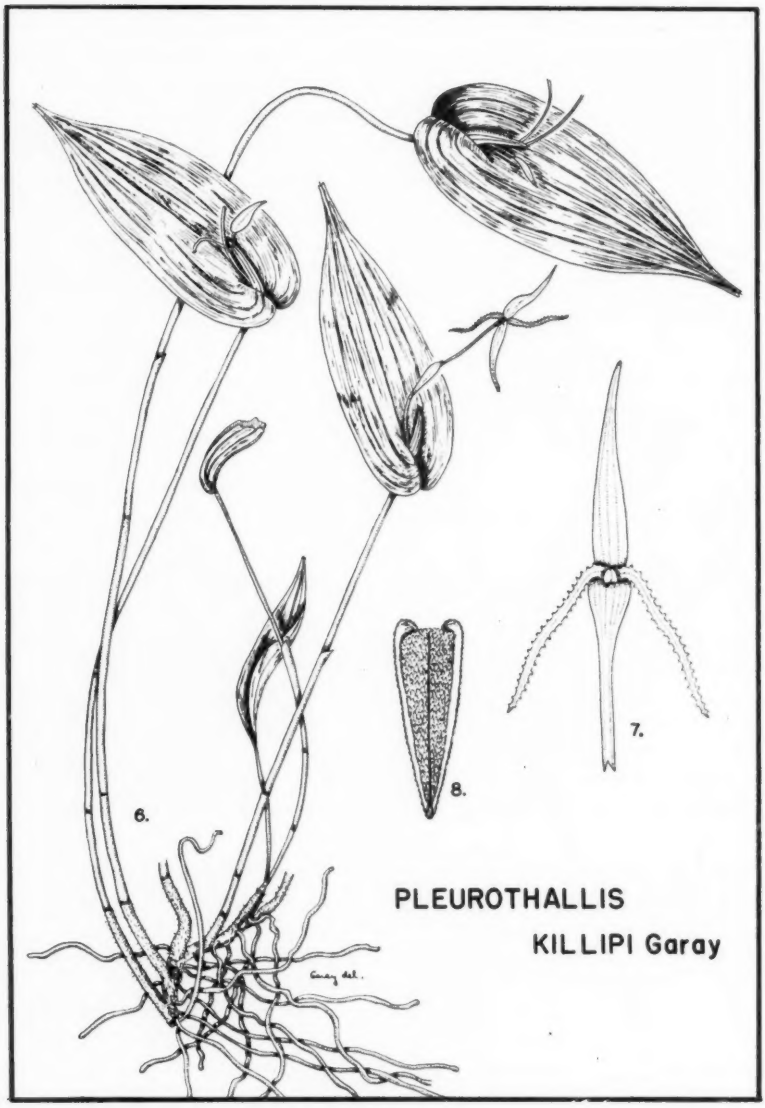


FIG. 6. General habit of plant × 2/3. FIG. 7. Expanded flower × 1.5.
FIG. 8. Lip × 3.5.

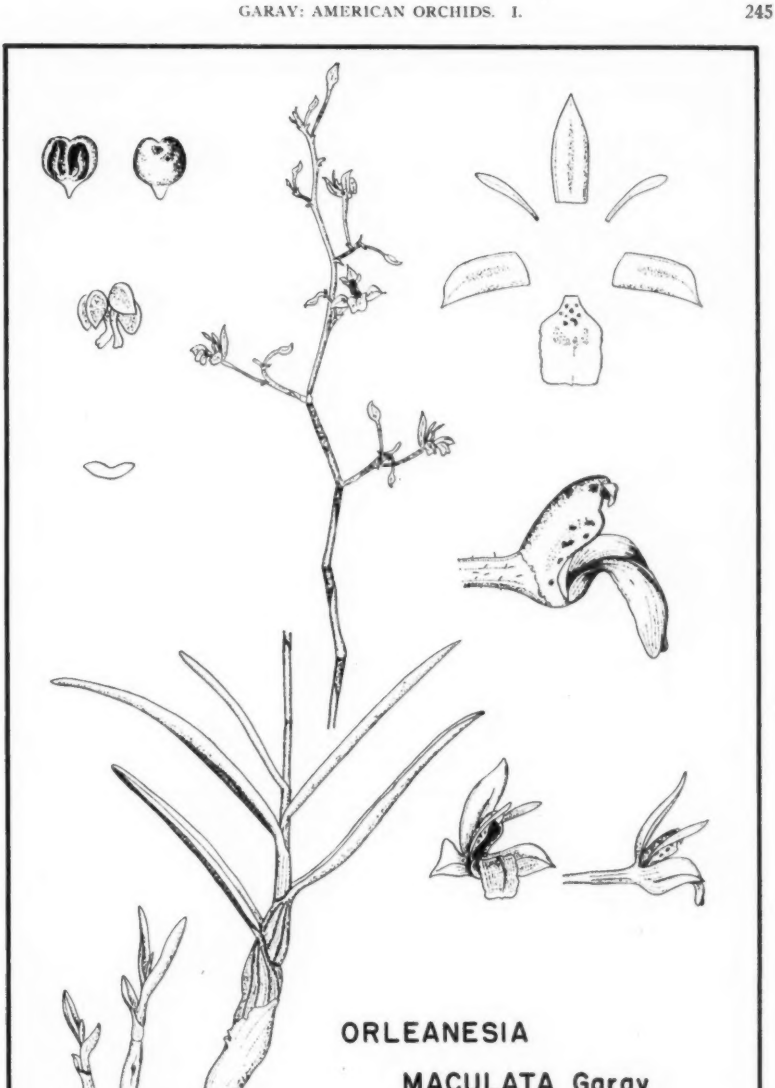


FIG. 9. General habit of plant × 2/3 and floral details × 1.5.

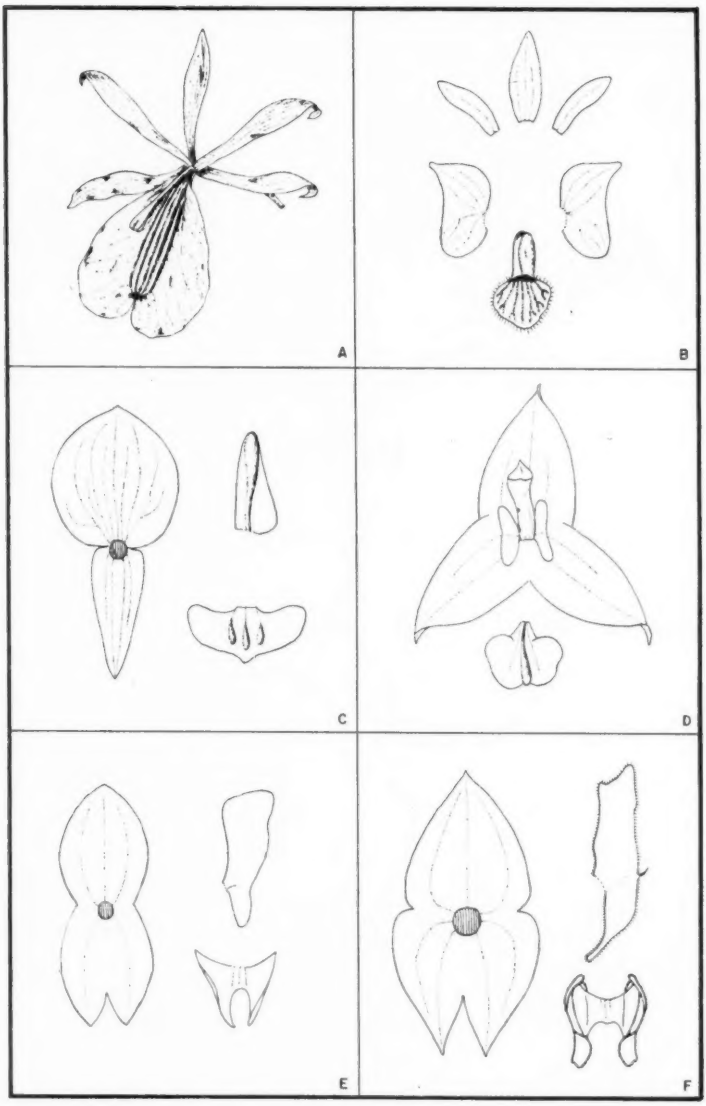


FIG. 10. *A. Sobralia kermesina*, a flower × 2/3. *B. Cranichis Asplundii*, floral parts × 3. *C. Lepanthes palmaritoensis*, sepals × 3, petal × 16, and lip × 9. *D. Lepanthes pendens*, a flower × 10. *E. Lepanthes hemirhoda*, sepals × 8, petals and lip × 7. *F. Lepanthes macrantha*, sepals × 3, petal × 8, lip × 7.

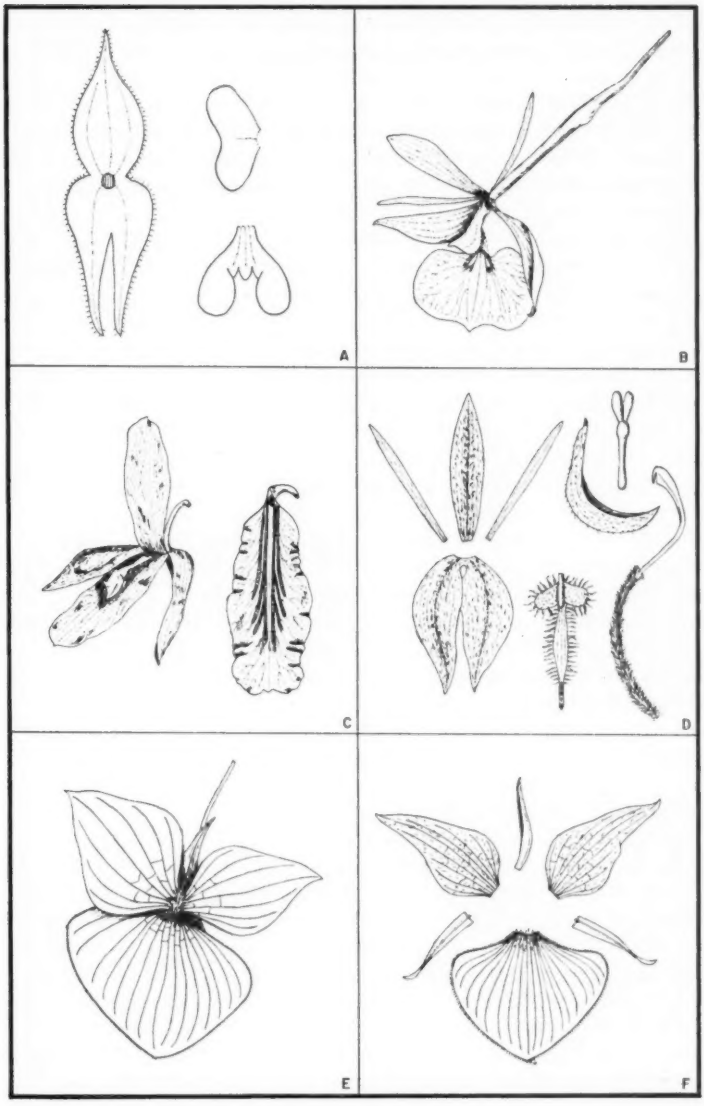


FIG. 11. *A. Lepanthes Vareschii*, sepals × 6, petals and lip × 10. *B. Epidendrum Cuatrecasasii*, a flower × 1.5. *C. Rodriguesia Strobelii*, an expanded flower × 1, lip × 1.5. *D. Polycycnis ornata*, flower parts slightly enlarged. *E. Telipogon ochraceus*, an expanded flower × 1.25. *F. Telipogon roseus*, floral details × 1.25.

and its inflorescence is an abbreviated cluster of flowers. *Sobralia scopulorum* Rchb.f. from Bolivia is also of this relationship but has a short, dense, lateral inflorescence, with flowers of different shape and texture.

Cranichis Asplundii Garay, sp. nov. Fig. 10 B

Terrestris, erecta usque ad 40 cm. alta; radicibus filiformibus, leviter flexuosis, pilosis; foliis 1–2 sub-basilaribus, ovatis, acuminatis, basi in petiolum 2 cm. longum attenuatis, lamina 4–5 cm. longa, 1.8–2 cm. lata; caulibus elongatis, teretibus, remote 4-vaginatis, glabris; inflorescentiis cylindraceis densifloris cum rachide leviter puberula 4–6 cm. longis; bracteis oblongis, acuminatis, ovariorum pedicellatorum dimidium aequantibus; floribus in genere inter mediocribus, glabris; sepalo postico ovato-oblongo, acuto, concavo, 3-nervio, nervo mediano dorso carinato, 5 mm. longo, 2 mm. lato; sepalis lateralibus transverse pandurato-subquadratis, apice leviter falcatis, acutis, basi subrotundis, obtusis, 5-nerviis, 4 mm. longis, 5 mm. latis; petalis oblongo-linearibus, leviter falcatis, uninerviis, 4.5 mm. longis, 1 mm. latis; labello suborbiculari, obtuso, basi in saccum calcariformem producto, margine distincte ciliolato; disco cum nervis 7, valde incrassatis ornato; lamina labelli 3 mm. longa et lata; sacculo 2 mm. longo; ovariis cylindraceis, pubescentibus, cum pedicellis 1 cm. longis.

Ecuador: Prov. Napo-Pastaza, between Cosanga and Guacamayo. On the ground. Flowers white. Oct. 27, 1939. Coll. *E. Asplund No. 9553.* Type in the herbarium of the State Museum of Natural History, Stockholm, Sweden.

Cranichis Asplundii most closely resembles three other species of the genus. It is larger than the Costa Rican *C. saccata* Ames and its flowers have differently shaped lateral sepals and lip. The Mexican *C. gracilis* L.O. Wms. and the West Indian *C. ventricosa* Griseb. also differ from *C. Asplundii* in flower structure, *C. gracilis* with a quite dissimilar lip and an auriculate column, *C. ventricosa* with a distinctly three-lobed lip.

Spiranthes decora Garay, sp. nov. Figs. 1–5

Terrestris, erecta, valida, usque ad 50 cm. alta; radicibus fasciculatis, carnosis, ut videtur glabris; foliis rosulatis erectis, longe petiolatis, ovato-lanceolatis, acuminatis, glabris, lamina superficie marmorata, subtus pallidiore; pedicellis 8 cm. longis, laminis 8–12 cm. longis, 2–4.5 cm. latis; caulibus erectis, remote vaginatis cum spica subsecunda, usque ad 50 cm. longis; vaginis primum caulibus adpressis deinde dilatatis, longe lanceolato-acuminatis, sursum decrescentibus; bracteis lanceolatis, acuminatis, ovariis pedicellatis aequantibus seu sensim longioribus, ad 3 cm. longis; floribus ut videtur viridibus, magnis, glanduloso-pubescentibus; sepalo postico cum petalis galeam formanti, oblanceolato-oblongo, acuto, valde concavo, intus glabro, extus glanduloso-pubescenti, 19 mm. longo, 5 mm. lato; sepalis lateralibus lineari-oblongis, apicem versus sensim dilatatis, basi in pseudocalcar ovario omnino adnatum mentum acutum formantibus decurrentibus, 30 mm. longis, apice 2 mm., basi 4 mm. latis; petalis filiformibus cum sepalo postico galeam formantibus, apice leviter dilatatis, margine anteriore glanduloso-ciliatis, 19 mm.

longis, basi 1 mm., apice 2 mm. latis; labello unguiculato, a basi sagittata oblongo-ligulato, apice trilobato; lobis lateralibus depauperatis, more dentiformibus, lobo intermedio transverse subrotundo vel reniformi, margine crenulato; disco ad junctionem loborum lateralium callo V-formi ornato; toto labello 23 mm. longo antice 6 mm. lato, omnino glabro solum supra basin parce piloso; columna gracili; rostello prominenti subtruncato; ovariis oblongis brevissime pedicellatis, glanduloso-pubescentibus, usque ad 2 cm. longis.

Colombia: Eastern Cordillera; Dept. Santander; Mesa de los Santos; alt. 1500 meters. Leaves dark green, variegated above with pale green center and pale green spots; segments light green. On floor of dense woods. Dec. 11–15, 1926. Coll. *E. P. Killip and A. C. Smith No. 15318* (Type). Type in the author's herbarium No. 3446. Duplicate type in U.S. National Herbarium No. 1953081.

Spiranthes decora differs from *Spiranthes Wendlandiana*[3] in its larger flowers, shorter and more acute pseudocalcar, and different lip; from the Venezuelan *S. maculata* (Rolfe) Schweinf. in its larger and differently colored flowers, smaller and acuminate leaves, and the shape of the lip.

Erythrodes Ortgiesii (Hort.) Garay, comb. nov.

Syn.: *Anoectochilus Ortgiesii* Hort. Flor. and Pomol. p. 243. Nov. 1872. cum. xyl. Hort. ex Van-Geert, Cat. No. 70, 1873.
Physurus Ortgiesii Rchb.f. *in* Gardeners' Chron. 177. 1873.

When the type of *Physurus Ortgiesii* Rchb.f. was kindly loaned to the writer by the Reichenbach Herbarium, it was possible to verify that a recent collection from Colombia, Department Santander (*N.C. Fassett No. 25166*) is referable to this species. Reichenbach's description was of little help in identification, since it makes a very broad statement regarding habitat ("the plant is reported to grow at a high elevation in New Granada") and is based on a type which consists only of the tip of an inflorescence and a single leaf. It therefore seems advisable to amplify the original description.

Plant 20–35 cm. tall. Leaves broadly ovate, acuminate, cuneate at the base, distinctly petiolate; petiole up to 1.5 cm. long; blade 4–6 cm. long, 2.5–3 cm. broad. Peduncle erect, distinctly 3 (2–4)-vaginate. Inflorescence cylindrical, very compact and many-flowered, 3–4.5 cm. long. Sepals and petals 5 mm. long. Lip 7 mm. long. Spur and ovary rather sharply curved, geniculate.

Since the genus *Physurus* is inseparable from *Erythrodes*, the above transfer is necessary.

Physosiphon Bangii (Schltr.) Garay, comb. nov.

Syn.: *Masdevallia Bangii* Schltr. *in* Fedde Rep. Beih. 10: 41. 1922.

In connection with the preparation of a monograph of the *Pleurothallidinae*, the writer has suspected that *Masdevallia Bangii*, for which Schlechter proposed

[3] ***Spiranthes Wendlandiana*** *(Krzl.) Garay, comb. nov. in hoc loco.*
Syn.: Pelexia Wendlandiana Krzl. in Gardeners' Chron. 1: 426. 1892.
Pelexia Lehmanniana Krzl. in Engl. Bot. Jahrb. 26: 500. 1899.

a new section "*Trichotosiphon*", is a member of the genus *Physosiphon*. When he was able to examine the type collection (*Bang. 2424*!) in the Smithsonian Institution, he found confirmation of his belief. *Physosiphon Bangii*, which was described from Bolivia, closely resembles the Venezuelan *P. Lansbergii* (Rchb.f.) L.O.Wms., from which it differs in having carinate sepals, entire petals, and a dissimilar lip.

Lepanthes hemirhoda Garay, sp. nov. Fig. 10 E

Epiphytica, caespitosa, mediocri; radicibus filiformibus, flexuosis, glabris; caulibus teretibus, erectis, distante cum vaginis imbricatis, tubulosis, sursum ampliatis, parce muriculatis, omnino obtectis, 7.5 cm. longis; folio singulo, ovato-lanceolato, utrinque attenuato, acuminato, basi brevissime petiolato, satis carnoso, marginato, 4.5 cm. longo, 1 cm. lato; inflorescentiis 1–3-nis, valde fractiflexis, foliorum dimidio brevioribus, paucifloris; floribus satis minutis, glabris; sepalo postico ovato, obtuso vel acuto, 3-nervio, intense purpureo, 2.5 mm. longo, 2 mm. lato; sepalis lateralibus cum sepalo postico breviter et inter se usque ad 1/3 partem apicalem connatis, bifidis, ovatis vel ovato-oblongis, acutis, uninerviis, glabris, albidis vel pallide roseolis, 2.5 mm. longis, 2 mm. latis; petalis transverse bilobis, uninervis; parte superiore (sepalum posticum versus) oblique cuneato-subquadrato, leviter curvato, intense purpureo; lobo antico valde abbreviato, oblongo, obtuso vel subacuto, pallide roseolo; 2.5 mm. latis, ad nervum medianum 1 mm. longis; labello bipartito, 3-nervio, partitionibus dolabriformibus, acutis vel acuminatis, petalis dimidio brevioribus; columna gracili; ovariis graciliter pedicellatis.

Colombia: Cordillera Oriental; Dept. Norte de Santander; region del Sarare; 1800–2200 meters. Oct. 18, 1941. Coll. *J. Cuatrecasas, R. E. Schultes & E. Smith No. 12458*. Type in the herbarium of the United States National Museum No. 1850752.

Lepanthes hemirhoda somewhat resembles the Venezuelan *L. Aquila-Borussiae* Rchb.f., but is certainly very distinct. The sepals in the latter species are acuminate (acute to obtuse in *L. hemirhoda*) and free almost to the base; the posterior lobe of the petals is erosulo-bidentate whereas in the new species it is acute to obtuse, and the lip is quite different in the two species.

Lepanthes macrantha Garay, sp. nov. Fig. 10 F

Epiphytica, caespitosa, usque ad 20 cm. alta; radicibus filiformibus, flexuosis, glabris; caulibus suberectis, gracilibus, remote vaginatis, 10–15 cm. longis; vaginis adpressis, sursum leviter dilatatis, ostiolatis, ostiolis longe acuminatis, margine muriculatis; foliis pergameneis, in exsiccatione rugulosis, ovatis, ad 1/3 partem apicalem abrupte contractis deinde lanceolatis, acuminatis, apice distincte mucronato-tridentatis, 9 cm. longis, ad medium 3 cm. latis; inflorescentiis folia dimidio superantibus, singulis vel binis, longe pedunculatis, pedunculo gracili, medio vaginato, rachide secundiflora; floribus

inter maximos generis, ut videtur flavescentibus; sepalo postico cum sepalis lateralibus alte connato, ovato-triangulari, acuto vel abrupte acuminato, distincte 3-nervio, glabro, 7 mm. longo, 6 mm. lato; sepalis lateralibus usque ad medium connatis, bifidis, dorsali simillimis, binerviis, 7 mm. longis, 7 mm. latis; petalis bipartitis, partitione postica oblonga, truncata, partitione antica ovato-lanceolata, subfalcata, acuminata, margine ciliolata, ad medium unicirrhosa, 4.25 mm. lata, 1 mm. longa; labello bilobo, lobis dolabriformibus, minutissime puberulis, 2 mm. longis, ovariis graciliter pedicellatis, bracteis tubulosis, minutissime ciliolatis triplo longioribus.

Colombia: Cordillera Oriental; Dept. Norte de Santander; region del Sarare; entre el Alto del Loro y el Alto de Santa Ines, bosques; 1800–2200 meters. 18, 20, 21 octubre 1941. Coll. *J. Cuatrecasas, R. E. Schultes, E. Smith No. 12403.* Type in the herbarium of the United States National Museum No. 1850968.

This new species bears resemblance in its vegetative characteristics to *L. papyrophylla* Rchb.f., but the latter species possesses small flowers, unappendaged semirotund petals. The Costa Rican *L. elata* Rchb.f. is also of this relationship, but in that species the sepals are narrow-triangular and the lateral ones free almost to the base, and the petals have a thickened margin.

Lepanthes palmaritoensis Garay, sp. nov. Fig. 10 C

Epiphytica, pendens, usque ad 50 cm. longa; radicibus axillaribus, filiformibus, flexuosis, glabris; caulibus primariis longe repentibus, vaginis amplis, costatis, hispidis omnino obtectis; caulibus secundariis abbreviatis, distichis, omnino in vaginam unam hispidulam inclusis, ca. 1 mm. longis; foliis oblongis, obtusis, in exsiccatione valde rugulosis, margine distincte longe ciliolatis, 8 mm. longis, 5 mm. latis; inflorescentiis abbreviatis, unifloris, folia dimidio aequantibus; floribus pro planta satis magnis, fulvis, purpureo-striatis, glabris; bracteis tubulosis, obliquis, amplis, margine longe ciliatis, pedicellis dimidio brevioribus; sepalo postico orbiculari, 7-nervio, 7 mm. longo, 6.5 mm. lato; sepalis lateralibus in synsepalum ovato-lanceolatum, acutum, 5-nervium omnino connatis, 7 mm. longis, 2 mm. latis; petalis abbreviatis, lanceolato-triangularibus, uninerviis, nervo valde incrassato prominenti, 1 mm. longis, 0.5 mm. latis; labello integro, obscure trilobo, reniformi-cordato, lobis lateralibus oblongis, obtusis, postice cordatis, lobo intermedio obscuro, triangulo, obtuso, disco cum nervis 3 incrassatis ornato; toto labello 0.75 mm. longo, 1.75 mm. lato; columna humili; ovariis pedicellatis bracteas duplo superantibus.

Colombia: Dept. Cundinamarca; Cordillera Oriental; east side of the Palmarito Valley, 8 km. east of Gutierrez, 50 km. south of Bogota. Temperate forest. Alt. 2650 meters. Epiphyte, hanging; perianth yellow, red-striped; leaves ciliate. July 22, 1944. Coll. *Martin L. Grant No. 9628.* Type in the herbarium of the United States National Museum No. 2106878. Isotype in the author's herbarium No. 3092.

Lepanthes palmaritoensis is most closely related to *L. saccosepala* Smith & Harris. The species differs in the shape of the lateral sepals and of the lip, and in the character of the leaves which in *L. palmaritoensis* are glabrous on both surfaces, in *L. saccosepala* are covered throughout with soft hairs.

Lepanthes pendens Garay, sp. nov. Fig. 10 D

Epiphytica, pendulosa, usque ad 50 cm. longa; radicibus axillaribus, longe-filiformibus, leviter flexuosis, glabris; caulibus primariis longe repentibus, vaginis amplis, costatis, muriculato-hispidulis imbricatisque omnino obtectis; caulibus secundariis distichis, valde abbreviatis, omnino in vagina unica inclusis, 1 mm. longis; foliis oblongis ellipticisve, obtusis, pergameneis, usque ad 1 cm. longis, 5 mm. latis; inflorescentiis uni- seu bifloris, brevissime pedunculatis, 2 mm. longis; floribus minimis, purpurascentibus; bracteis obliquis, tubulosis, supra dilatatis, glabris; sepalis inter se simillimis, triangulato-ovatis, acutis, apice reflexis, glabris; sepalo postico 3-nervio, 2.5 mm. longo, 1.75 mm. lato; sepalis lateralibus binerviis, 2.5 mm. longis, 1.25 mm. latis; petalis transversis, bilobis, lobis aequalibus, oblongis, obtusis, 0.25 mm. longis, 1 mm. latis; labello breviter lateque unguiculato, deinde cordato-reniformi, antice retuso, glabro, disco 3-nervio, nervo mediano apicem versus incrassato donato, 1 mm. longo, 1.25 mm. lato; columna gracili, apice leviter incrassata; clinandrio integerrimo; ovariis pedicellatis bracteis duplo longioribus.

Colombia: Dept. Cundinamarca; Cordillera Oriental; Alto de Tunque, 11 km. east of Guitierrez, 50 km. south of Bogota. Temperate forest. Alt. 2515 meters. Epiphyte, pendent; perianth red with green margins. July 31, 1944. Coll. *Martin L. Grant No. 9770.* Type in the herbarium of the United States National Museum No. 2106923. Isotype in the author's herbarium No. 3264.

Lepanthes pendens belongs to the section "*Caulescentes*", all species of which are very similar in habit. Our new species is distinct in its floral structure.

Lepanthes Vareschii Garay, sp. nov. Fig. 11 A

Epiphytica vel saxicola, usque ad 10 cm. alta; radicibus filiformibus flexuosis, glabris; caulibus caespitosis, gracilibus, suberectis vel leviter flexuosis, distante 4–6-vaginatis; vaginis per totam longitudinem adpressis, tantum ostiolis densissime hispidulis, abrupte dilatatis; foliis lanceolatis vel ovato-lanceolatis, acutis, apice minutissime tridenticulatis, basi in petiolum 1–2 mm. longum attenuatis, 2.5–3.5 cm. longis, 6–8 mm. latis; inflorescentiis singulis vel geminis, leviter fractiflexis, paucifloris, foliis dimidio brevioribus; floribus succedaneis, flavidis, inter minores generis; sepalo postico ovato-lanceolato, acuminato, 3-nervio, nervo mediano incrassato-carinato, margine distincte ciliolato, 4 mm. longo, 2 mm. lato; sepalis lateralibus ad 1/3 partem basilarem inter se connatis, lanceolatis, acuminatis, uninerviis, nervis dorso carinatis, margine ciliolatis, 4 mm. longis, antice 1 mm. basin versus 2.25 mm. latis; petalis transveris, bilobis, lobis aequalibus, oblongis, seu reniformis

et antice sinuosis, uninerviis, 0.5 mm. longis, 1.5 mm. latis; labello a cuneata basi trilobo, lobis lateralibus ovatis, obtusis, lobo intermedio minutissimo, lobis lateralibus multoties brevioribus, disco ad basin 3-nervio, toto labello 1.5 mm. longo; columna gracili apicem versus capitato-dilatata, 1.5 mm. longa; ovariis pedicellis aequilongis, bracteisque duplo longioribus.

Venezuela: Podocarpetum an Paramo de Monsalves; 3190 meters. Edo. Merida. November 10, 1952. Coll. *Dr. V. Vareschi No. 2306.* Type in the author's herbarium No. 3473. Isotype in the National Herbarium of Venezuela.

The ciliolate sepals and unappendaged petals readily separate this new species from *L. mucronata* Lindl. *Lepanthes nubicola* Rchb.f., another similar taxon, has acuminate petals and a dolabriform lip, in contrast to the obtuse petals and ovate lip of *L. Vareschii.* Otherwise the three are quite closely related.

Pleurothallis declivis Lindl. Fol. Orch. Pleuroth. p. 36. 1859.

Syn.: *Humboldtia declivis* O. Ktze. Rev. Gen. Pt. 2, p. 667. 1891.
Physosiphon inaequisepalus Schltr. *in* Fedde Rep. Beih. 9: 50. 1921.

The species *Pleurothallis declivis* and *Physosiphon inaequisepalus* have been distinguished on the basis of calyx-structure. The first is described as having its dorsal sepal free from the lateral sepals, while according to Schlechter, the second has a short calyx-tube. Neither description can be considered entirely accurate, since the dorsal and lateral sepals are somewhat coherent in both species, but not for more than one and a half millimeters. This condition, which is not unusual in the genus *Pleurothallis*, is evident in Schlechter's drawings of *Physosiphon inaequisepalus* also, but it can scarcely be called a tube. A careful examination of Jameson's material of *Pleurothallis declivis* (Type!) in the Reichenbach herbarium at Vienna, the floral analysis of this species in the Lindley herbarium at Kew, and comparisons of these with Schlechter's description and drawings make it apparent that these concepts are identical.

Pleurothallis Johnsonii Ames Sched. Orch. 2: 21. 1923.

Syn.: *Brenesia costaricensis* Schltr. *in* Fedde Rep. Beih. 19: 200. 1923.

Pleurothallis Johnsonii is a rather remarkable species. In its typical form, which is more common in Guatemala, the inflorescence appears to be terminal. However, several collections from Costa Rica, which are morphologically the same, appear to have inflorescences arising laterally at the base of the secondary stem. This latter form has been described by Schlechter as a new genus *Brenesia.* There is a collection in the Reichenbach herbarium made in Costa Rica by Endres and another from Honduras in the Ames herbarium, each with both terminal and lateral inflorescences. The appearance of lateral inflorescences in the subtribe *Pleurothallidinae* is quite unusual, but we have similar cases in other genera such as *Epidendrum, Dendrobium, Coelogyne,* etc. It seems unwise to establish a new genus on a single vegetative character which occurs rather rarely.

Recent collections submitted by Mrs. R. Oberg extend the range of the species to southern Mexico, where both types were observed, although not on the same rootstalk.

Pleurothallis Killipi Garay, sp. nov. Figs. 6–8

Terrestris, saxicola, 25–30 cm. alta; radicibus filiformibus, elongatis, flexuosis, glabris; caulibus ascendentibus, teretibus, in medio univaginatis, basin et cum rhizomate valde abbreviato hispidulis, 15–20 cm. longis, 2–3 mm. crassis; foliis ovatis, abrupte acuminatis, basi valde cordatis, satis coriaceis, 7.5–9 cm. longis, 2.5–3.5 cm. latis; inflorescentiis e spatha lanceolata, leviter falcata, 2 cm. longa, aggregatis, unifloris, satis longe pedunculatis; pedunculis 2 cm. longis; bractea magna, tubulosa, acuta, 12 mm. longa; floribus inversis, purpureo-punctatis (ex collectore), satis magnis; sepalo postico lanceolato-acuminato, leviter concavo, 3-nervio, glabro, 2 cm. longo, 3 mm. lato; sepalis lateralibus in synsepalum apice breviter bifidum, anguste lanceolatum, omnino connatis, 6-nerviis, glabris, sepalo postico aequilongis seu paulo brevioribus, antice 1 mm., basin versus 4 mm. latis; petalis filiformibus, acuminatis, uninerviis, margine grosse dentatis, 1.5 cm. longis, 1 mm. latis; labello cuneato-triangulo-hastato, acuto, basin leviter genuflexo, margine papilloso, disco densissime verruculoso, 8 mm. longo, ad basin 3 mm. lato; columna humili, basi in pedem brevissimum producta; ovariis cylindraceis, longe graciliterque pedicellatis, cum pedicellis 2.5 cm. longis.

Colombia: Dept. Cundinamarca; Los Gaques, western slope of Paramo de Guasca; alt. about 3250 meters. Terrestrial. Five segments greenish, pink tinged; lip pink-spotted; column yellow. In woods. March 12, 1939. Coll. *E. P. Killip No. 34061.* Type in the United States National Museum No. 1770925. Isotype in the author's herbarium No. 3320.

This new species appears to be clearly distinct from all others, though it approaches *P. gratiosa* Rchb.f. in many ways. However, the two can be easily distinguished since *P. Killipi* is a much coarser plant with an entirely different lip.

Pleurothallis pachypus (Lehm. & Krzl.) Garay, comb. nov.

Syn.: *Stelis pachypus* Lehm. & Krzl. *in* Engl. Bot. Jahrb. 26: 447. 1899.

Several sheets of the type collection of *Stelis pachypus* have been examined through the courtesy of the New York Botanical Garden and the Smithsonian Institution. This taxon is unquestionably not a member of the genus *Stelis*, since its column is elongate with a foot-like extension of the base, the petals are large and of tenuous texture, and the lip is articulated with the column-foot. In the genus *Stelis*, these structures are quite otherwise in nature. In fact, on the basis of its vegetative appearance, coupled with the morphological characters of the individual floral segments, the species fits very well into a large group of *Pleurothallis* species which are often very similar vegetatively, a group including *Pleurothallis velaticaulis* Rchb.f. and *Pleurothallis pulchella* Lindl.

Pleurothallis Tunguraguae Lehm. & Krzl.

var. ***minor*** Garay, var. nov.

A typo habitu humiliori, labello ecalloso differt.

Planta ut videtur saxicola, caespitosa, 15–25 cm. alta; caulibus e cataphyllis plurimis, parce evanidis, fasciculatis, potius breviter ascendentibus, in medio vaginatis, 7–12 cm. longis; foliis oblongis, satis coriaceis, in exsiccatione margine leviter revolutis, apicem versus sensim conduplicatis, basin versus in petiolum conduplicatum angustatis, 5–10 cm. longis, 1–2.5 cm. latis; inflorescentiis 1–3-nis, folia superantibus,; floribus illis typi simillimis et aequimagnis excepto apice labelli leviter pulvinato nec callifero incrassato.

Colombia: Facatatiosa; alt. 2400 meters. Sept. 29, 1918. Coll. *Bro. Aristide-Joseph No. A194.* Type in the herbarium of the United States National Museum No. 888402.

Epidendrum Cuatrecasasii Garay, sp. nov. Fig. 11 B

Epiphytica, suberecta, gracili, usque ad 25 cm. alta; radicibus filiformibus, flexuosis, glabris; caulibus elongatis, leviter compressis, foliosis; foliis oblongo-ligulatis, acuminatis, pergameneis, mucronatis, basi caulem amplectentibus, usque ad 10 cm. longis, 4–7 mm. latis; inflorescentiis supra basin caulium lateralibus, valde abbreviatis, ut videtur unifloris; floribus succedaneis, flavidis, satis carnosis, magnis; bracteis minutissimis, ovariis pedicellatis multoties brevioribus; sepalo postico oblongo-obovato, acuto, 5-nervio, nervis 3 dorso valde prominentibus, 1 cm. longo, 3 mm. lato; sepalis lateralibus obliquis, dorsali simillimis, 5-nerviis, nervis omnibus valde prominentibus, acutis, basi columnae breviter adnatis, 1.1 cm. longis, 4 mm. latis; labello columnae omnino adnato, cordato-reniformi, antice retuso cum apiculo, disco papuloso incrassato, nervis omnibus valde prominentibus, ante columnam callis 2 oblongis ornato; toto labello 8 mm. longo, 13 mm. lato; columna satis crassa, subclavata, antice lobulosa; clinandrio denticulato, satis alto; ovariis fusiformibus, brevissime pedicellatis, cum pedicellis 2.4 cm. longis.

Colombia: Dept. del Valle; Río Calima (region del Choco); La Trojita; alt. 5–50 meters. 19 febr. 10 mar. 1944. Coll. *J. Cuatrecasas No. 16252.* Type in the herbarium of the United States National Museum No. 1906451.

Epidendrum Cuatrecasasii is a member of the section *Pleuranthium* which is considered, by some, to be a distinct genus. Careful study reveals no substantial evidence in support of this idea. This new species is perhaps closest to *E. pileatum* Rchb.f. which has much smaller flowers and a very dissimilar lip.

Scaphyglottis flaccida (Krzl.) Garay, comb. nov.

Syn.: *Ornithidium flaccidum* Krzl. *in* Fedde Rep. 25: 31. 1927.

During the course of identification of Bolivian orchids, it has become evident that the taxon described as *Ornithidium flaccidum* cannot be a member of the subtribe *Maxillarieae*, to which the genus *Ornithidium* belongs. In this subtribe, inflorescences are either lateral or axillary, but never terminal.

In contrast, the type specimen of *O. flaccidum* (*Buchtien No. 526*! in the herbarium of the Smithsonian Institution) shows a completely terminal inflorescence. Furthermore, it finds a fitting place in the subtribe *Ponereae* because of several other characteristics, such as its appendiculate pollinia, the duplicative venation of its leaves, its distinct column-foot, and dorsally ascendant clinandium. Finally, the type specimen shows all the characters attributed to the genus *Scaphyglottis*, in the subtribe *Ponereae*.

Orleanesia maculata Garay, sp. nov. Fig. 9

Epiphytica, erecta, usque ad 65 cm. alta; rhizomate abbreviato, leviter ascendenti, crasse-carnoso lignosoque; radicibus perpaucis, leviter flexuosis, glabris; caulibus ascendentibus, fusiformibus, in exsiccatione valde sulcatis, primum seu infra vaginis ternis, papyraceis, valde adpressis obtectis, deinde vaginis distichis, foliiferis, quinis donatis; foliis oblongo-ligulatis, crasse carnosis, semiconduplicatis, dorso distincte carinatis, 5–9 cm. longis, 5–8 mm. latis; inflorescentiis terminalibus, paniculatis, leviter compressis, usque ad 35 cm. longis; panicula fractiflexa, ramulis abbreviatis, paucifloris; floribus satis magnis, 2 cm. in diam.; sepalis petalisque viridibus brunneo suffusis, labello et columna viridi cum maculis roseo-purpureis; sepalo postico ovato-oblongo, acuto, sensim concavo, 9–10 mm. longo, 2–3 mm. lato; sepalis lateralibus obliquis, dorsali simillimis, 7–8 mm. longis, 2–3 mm. latis; petalis oblanceolato-linearibus, acutis, subfalcatis, basin versus cuneato-attenuatis, 6–7 mm. longis, 0.5–1 mm. latis; labello genuflexo, a cuneata basi quadrato, antice truncato, sinuoso cum apiculo interjecto, disco in basi sub lente minutissime puberulo, 7 mm. longo, 5 mm. lato; columna humili, crassa, per totam longitudinem late alata, basi in pedem leviter incurvum producta, 5 mm. alta; ovariis cylindraceis, satis longe pedicellatis, cum pedicellis 1.5 cm. longis.

Venezuela: Salon Timerla. December 1954. Coll. *G. C. K. Dunsterville No. 240.* Type in the author's herbarium No. 4277.

Among the species of *Orleanesia*, the Brazilian *O. yauaperyensis* Rodr. and *O. peruviana* Schweinf. are the only ones which might be confused with this new species. But *O. maculata* is altogether smaller than *O. yauaperyensis*, with smaller flowers and a quadrate lip, while *O. peruviana* differs in its pendulous inflorescence and the semirotund lip of its flower.

It is obvious from this discussion that the writer does not accept the genus *Huebneria* which was established by Schlechter for *Orleanesia yauaperyensis*. It appears scarcely defensible to distinguish two genera solely on the basis of an abbreviated raceme versus an elongate panicle.

Polycycnis ornata Garay, sp. nov. Fig. 11 D

Epiphytica, pendenti; radicibus filiformibus, leviter flexuosis, glabris; pseudobulbis orbicularibus, in exsiccatione sensim rugulosis, apice bifoliatis, 3.5 cm. altis crassisque; foliis ovatis, ellipticis, supra canaliculatis, acuminatis,

basi distincte petiolatis, subchartaceis; petiolo 4–5 cm. longo, lamina 20 cm. longa, 8 cm. lata; inflorescentiis pendulis, usque ad 70 cm. longis; pedunculis 30 cm. longis, remote 5-vaginatis, puberulis; spica usque ad 40 cm. longa, satis dense multiflora; floribus conspicuis, pallide olivaceis, violaceo-maculatis; bracteis ovato-lanceolatis, acuminatis, ovariis pedicellatis dimidio brevioribus, dorso strigosis; sepalo postico reflexo, valde concavo-cucullato, latere viso falcato, vi expanso oblongo-lanceolato, acuto, 5-nervio, extus strigoso, intus glabro, expanso 1.8 cm. longo, 4 mm. lato; sepalis lateralibus ima basi paulo connatis, suberectis, in medio antice recurvis, ovato-lanceolatis, acutis vel acuminatis, 5-nerviis, nervo mediano valde incrassato carinaeformi, extus hispidulo-strigosis, intus glabris, 15 mm. longis, 6 mm. latis; petalis linearibus, suberectis, deinde in medio reflexis, 3-nerviis, 1.5 cm. longis, 1 mm. latis; labello basi columnae affixo, breviter unguiculato, deinde trilobato, lobis lateralibus ovato-oblongis, obtusis, scabridiusculis, margine densissime ciliis satis longis, albidis ornatis; lobo intermedio lanceolato, calloso-apiculato, scabridiusculo, margine dense ciliolato; disco mediano inter lobos laterales carina elevata, pubescenti ornato; toto labello 1.1 cm. longo, inter lobos laterales 7 mm. lato; columna arcuata, clavata, supra breviter bialata, 14 mm. longa, glabra; ovariis cylindricis, leviter arcuatis, densissime hispidulis, usque ad 2 cm. longis.

Ecuador: Prov. Napo-Pastaza, Ozoyacu (north of Archidona); alt. 1000 meters. On stump. Tep. light olive-green with violet dots, labellum white-tipped, towards base light violet, column green, yellowish white-tipped. 26 Oct. 1939. Coll. *Erik Asplund No. 9516.* Type in the herbarium of the State Museum of Natural History, Stockholm, Sweden.

Polycycnis ornata is very similar florally to *P. surinamensis* Schweinf., but very different vegetatively. *Polycycnis lepida* Linden & Rchb.f. differs from this new species in having a monophyllous pseudobulb and a large flower with a differently shaped and colored lip.

Maxillaria cuencana Garay, nom. nov.

Syn.: *Ornithidium luteorubrum* Lehm. & Krzl. *in* Engl. Bot. Jahrb. 26: 468. 1899.

Admittedly, the genus *Maxillaria* is highly polymorphic and there seems to be no reasonable way of separating out the genus *Ornithidium.* Therefore, its species must be transferred to the genus *Maxillaria.* In the case of *Ornithidium luteorubrum* Lehm. & Krzl., the transfer necessitates a change in specific name as well, since this taxon is different from the already established *Maxillaria luteorubra* (Lindl.) Rchb.f.

Maxillaria pleuranthoides (Schltr.) Garay, comb. nov.

Syn.: *Ornithidium pleuranthoides* Schltr. *in* Fedde Rep. 15: 55. 1917.

Maxillaria pleuranthoides was described from Ecuador; a recent collection (*F. R. Fosberg No. 20968!*) extends its range to Colombia Intendencia del Meta.

Rodriguesia Strobelii Garay, sp. nov. Fig. 11 C

Epiphytica, humili, ca. 10–15 cm. alta; radicibus satis crassis, fibrosis; pseudobulbis oblongo-ovoideis, in exsiccatione valde rugosis, monophyllis; foliis oblongis, obtusis, utrinque canaliculatis, valde coriaceis, 5–7 cm. longis, 1.5–2 cm. latis, foliis infrabulbosis geminis, illis pseudobulbosi simillimis; inflorescentiis abbreviatis, pauci- (2–3) floris; bracteis navicularibus, lanceolatis, ovariis pedicellatis dimidio brevioribus; floribus albidis cum labello lilacino-striato; sepalo postico ovato-oblongo, acuto, valde concavo, vi explanato 2 cm. longo, ca. 1 cm. lato; sepalis lateralibus usque ad apicem omnino connatis, dorsali simillimis, basi valde saccatis, 2 cm. longis, ca. 0.8 cm. latis; petalis ovato-oblongis, obtusis vel subacutis, 2.3 cm. longis, 0.8 cm. latis; labello oblongo, apice truncato retusoque, basi in calcar brevissime leviter falcatum, acutum, producto; disco lamellis 8, parallelis ornata; toto labello 2.25 cm. longo, 1 cm. lato; columna satis crassa, superne falculis valde prominentibus donata, 1.2 cm. alta; ovariis cylindraceis, breviter pedicellatis, cum pedicellis 8–10 mm. longis.

Ecuador: Sine loco speciali. Coll. *Mr. Strobel s.n.* Introduced and flowered in cultivation at the Montreal Botanical Garden February 15, 1955. Received through the courtesy of Dr. H. Teuscher, Curator of the Montreal Botanical Garden. Type in the author's herbarium No. 4335!

Rodriguesia Strobelii suggests *R. compacta* Schltr. from Costa Rica, but its smaller flowers with their lamellate lips differentiate it from the latter species.

Dipteranthus planifolius (Rchb.f.) Garay, comb. nov.

Syn.: *Ornithocephalus planifolius* Rchb.f. *in* Neederl. Kruidk. Arch. 4: 315. 1859.

Ornithocephalus obliquus Schnee *in* Rev. Fac. Ing. Agron. 1: 115. 1952.

Ornithocephalus planifolius exhibits all the characters of the genus *Dipteranthus* as described by Barbosa Rodrigues. Reichenbach himself must have been dissatisfied with the generic status of this species because he did not account for it in his revision of the genus *Ornithocephalus* in Walper's Annales Botanices, Vol. 6. The genus *Ornithocephalus* is characterized by equitant leaves and the lack of a pseudobulb, the inflorescence borne usually in the axils of the lower leaves. *Dipteranthus*, on the other hand, has no equitant leaves and possesses a well-developed pseudobulb with the inflorescence borne laterally at its base. A record of the type of *O. planifolius* (from the Reichenbach herbarium) clearly exhibits the latter characteristics.

Judging from the original description and illustration for *O. obliquus*, it is evident that this taxon agrees in every respect with the type of *O. planifolius*. Recently received specimens and excellent kodachromes sent by Mr. Dunsterville of Caracas confirm this view.

Dipteranthus planifolius is most closely allied to *D. ovatipetalus* Brade which was described from Rio de Janeiro. The genus is new to Venezuela and this species is apparently its only representative in the Andean region.

Telipogon ochraceus Garay, sp. nov. Fig. 11 E

(Caulescentes) Saxicola, usque ad 30 cm. alta; radicibus elongatis, satis fibrosis, flexuosis, glabris; caulibus ascendentibus, paucifoliatis, 5–8 cm. longis; foliis distichis, ovato-lanceolatis, coriaceis, in exsiccatione margine revolutis, dorso carinatis, basi caulem decurrentibus, 2.5 cm. longis, 1 cm. latis; caulibus suberectis, gracilibus, remote bivaginatis, teretibus, glabris, 13–20 cm. longis; inflorescentiis paucifloris, 1–4-nis; bracteis ovato-cucullatis, acutis, ovariis pedicellatis multoties brevioribus, 5 mm. longis; floribus satis magnis, ochraceis, 3.5 cm. in diam.; sepalis anguste-triangulis, acutis, dorso crasse carinatis, 1 cm. longis, 3.5 mm. latis, glabris; petalis ovato-triangulis, acuminatis, 7-nerviis, nervillis paucis supra basin, margine basin versus microscopice ciliolatis, supra nudis, 1.8–2 cm. longis, 13–15 mm. latis; labello deltoideo-triangulo, acuto, 17-nervio, nervillis perpaucis supra basin, margine ciliolato, disco ecalloso, supra basin hispidulo, 18 mm. longo, 24 mm. lato; columna humili, hispido-setacea; ovariis cylindraceis, costatis, cum pedicellis 21 mm. longis, glabris.

Colombia: Dept. Boyaca; cliff 5 km. southwest of Arcabuco. Petals dull yellow-brown with dark yellow veins; column dark red. Alt. 9000 ft. June 6, 1944. Coll. *N. C. Fassett No. 25298.* Type in the author's herbarium No. 3249. Isotype in the United States National Museum.

Telipogon ochraceus is closely related to the Venezuelan *T. Klotzscheanus* Rchb.f., but is distinguishable on the basis of a differently proportioned lip, the number of veins in the petals and lip, and the coloration of the entire flower. *T. Klotzscheanus* is described as having a yellow flower, internally uniform, externally decorated with blood-red stripes, its lip 21-nerved.

Telipogon roseus Garay, sp. nov. Fig. 11 F

(Caulescentes) Saxicola, erecta, usque ad 25 cm. alta; radicibus satis crassioribus, leviter flexuosis, inter folia jam mortua viviaque orientibus; caulibus bene foliatis, 10–12 cm. longis; foliis distichis, satis carnosis, lanceolatis, acuminatis, complicatis, dorso carinatis, basi caulem amplectentibus, 1–1.5 cm. longis, 5 mm. distantibus; scapis nunc terminalibus nunc ex axillis foliorum superiorum orientibus, erectis, teretibus, usque ad 15 cm. longis; inflorescentia pauciflora, racemosa, glabra; bracteis ovatis cucullatis, acuminatis acutisve, dorso carinatis, ovariis pedicellatis multoties brevioribus, 3–5 mm. longis; floribus mediocribus, ut videtur roseis; sepalis lanceolatis, acuminatis, 3-nerviis, dorso leviter carinatis, 10–11 mm. longis, 2.5 mm. latis; petalis ovato-triangulis, acuminatis, 9-nerviis, toto superficie densissime strigosis, 18 mm. longis, 8 mm. latis; labello deltoideo-triangulo, acuto, 19-nervio, nervis basin versus leviter incrassatis; disco nudo excepta basin parce hispidulo; margine labelli densissime ciliolato; toto labello 16 mm. longo, 20 mm. lato; columna abbreviata, dorso hispido-muriculata, antice echinacea; rostellum proboscideum, valde productum; ovariis cylindraceis, longe graciliterque pedicellatis, cum pedicellis 15 mm. longis.

Colombia: Dept. Cundinamarca; Cordillera Oriental; Río Blanco Valley, 8 km. west of Gutierrez. Shrubby hillside in temperate forest, on rocks. Perianth tan, with maroon veins. Alt. 2050 meters. July 28, 1944. Coll. *Martin L. Grant No. 9743.* Type in the author's herbarium No. 3253. Isotype in the United States National Museum.

There is considerable similarity between *T. roseus* and *T. gracilis* Schltr. on the one hand, and *T. hastatus* Rchb.f. on the other. *T. gracilis*, however, has larger leaves, differently shaped petals, and lip with fewer veins on the lip; and *T. hastatus* is characterized by a lip with a non-ciliate margin and more numerous veins. They are, therefore, both sufficiently distinct from *T. roseus* to necessitate the recognition of this taxon as a separate species.

CYTOTAXONOMY AND SEX DETERMINATION OF RUMEX PAUCIFOLIUS[1]

By Åskell Löve and Nina Sarkar

Abstract

The western North American dioecious species *Rumex paucifolius* is shown to be a tetraploid with $2n = 28$ chromosomes. It is the third tetraploid known within the subgenus *Acetosa*, and the first polyploid dioecious taxon of that group, the others having either $2n = 14\,♀, 15\,♂$ (*R. Acetosa* and relatives), or $2n = 8\,♀, 9\,♂$ (*R. hastatulus*). The sex chromosomes of *R. paucifolius* are of the *XX:XY* type, the male sex being heterogametic. The *X* is a large chromosome, while the *Y* is the smallest chromosome of the complement. The mechanism of sex determination of *R. paucifolius* follows the *Melandrium–Acetosella* scheme with strongly epistatic male determinants in the *Y*-chromosome. Other dioecious *Acetosae* follow the *Drosophila–Acetosa* scheme of sex determination with a balance between the number of *X* and autosome complements, the *Y* being sexually inert. It is concluded from the observed cytogenetical and morphological differences that *R. paucifolius* should constitute a section of its own, *Paucifoliae*, which should be placed as far as possible from the section *Acetosa*, though within the same subgenus. The other American dioecious endemic, *R. hastatulus*, is placed in a subsection of the section *Acetosa*.

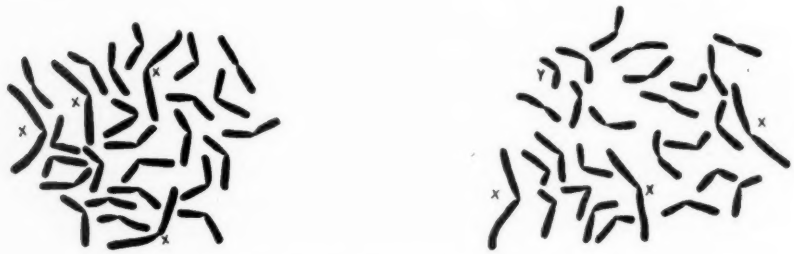
Of the many taxa of the genus *Rumex* which are indigenous and endemic on the North American continent, the species *R. hastatulus* Baldw. and *R. paucifolius* Nutting are of a particular interest from the points of view of evolution and classification. They are moderately gregarious in their habitats, and only the former has become such a weed that its original natural area is uncertain (27). Both species are morphologically very distinct and chorologically isolated, although there can be no doubt as to their belonging to the subgenus *Acetosa* rather than to the other recognized subgenera. And while both are dioecious, only the latter has been reported to have a tendency to androdioecism, a phenomenon rare within other dioecious taxa of this subgenus and contrary to what the established facts about sex mechanisms in the other species would lead one to expect.

Since the great importance of cytogenetical studies for the classification into natural units of the different groups of the subgenus *Acetosa* has been thoroughly established (8, 9, 10, 11, 12, 13, 24, 25), the present writers have undertaken an investigation of the cytology and sex determination of the western American endemic, *R. paucifolius*. The plants which were studied were grown from seeds collected by the senior writer in 1954 near the Timberline experimental garden of the Carnegie Institution of Washington, situated near the Tioga Pass in the Sierra Nevada in California. The specimens from which the seeds were taken belonged to the var. *gracilescens* Rech.f. typical of the southern and central Californian mountains. In nature, this taxon differs clearly from other populations, but the plants raised from seeds in the greenhouse at Winnipeg resembled the main type so closely that its genetical distinctiveness is doubted. However, this needs to be verified by experiment based on more material.

[1]*Manuscript received December 5, 1955.*
Contribution from the Department of Botany, University of Manitoba, Winnipeg, Manitoba.

The cytological studies were performed on root-tip material fixed in Levitsky's 8 : 2 solution (eight parts of 1% chromic acid, two parts of 10% formalin), sectioned, and stained in crystal violet according to the classical method (cf. 14) with the modification of the iodine-solution proposed by Suomalainen (29). This method gives excellent results in *Rumex* and the centromeres and other constrictions become distinct, while squashes in aceto-carmine or acetic-orcein do not give satisfactory results for studies on mitosis in this genus (26).

The chromosome number of female plants of *R. paucifolius* was found to be $2n = 28$, as shown in Fig. 1. The chromosomes are much smaller than those of other dioecious *Acetosae*, and even a little smaller than those of the subgenus *Acetosella*. While most of them are of about the same size, four are considerably larger than the others. In metaphase plates from male plants (Fig. 2) $2n = 28$ chromosomes are also found, but here only three of the larger ones are apparent, while one chromosome is slightly shorter than any of the others and without an equally sized partner. The chromosomes seem to be characterized by median and submedian centromeres only, a feature distinguishing the species from the Eurasiatic *Acetosae* with mainly submedian or subterminal rather than median centromeres. Centromere position of this kind is presumed to be an indication of primitiveness in *Rumex* (8), as it is in Ranunculaceae (5), *Allium* (4), *Crepis* (cf. 1), and some other groups, and it definitely separates this taxon from all extra-American dioecious *Rumex*.



FIGS. 1 and 2. Somatic chromosomes of *Rumex paucifolius*.
FIG. 1 (left). Female. FIG. 2 (right). Male. Magnification × 3300.

The basic number $x = 7$ may be said to be typical at least for the female plants of *R. Acetosa* and its closest relatives, but otherwise it is new for the subgenus *Acetosa* and known from the genus only in the subgenus *Acetosella*. However, morphological characters of *R. paucifolius* leave little doubt that it belongs to the subgenus *Acetosa*, and the morphology of the chromosomes does not indicate a closer relationship to any of the species of the subgenus *Acetosella*. There is an apparent similarity between the postulated mechanisms of sex determination in *R. paucifolius* and the subgenus *Acetosella*, but detailed study soon reveals that this must be mere coincidence.

Since meiotic divisions have not yet been studied in *R. paucifolius*, it has not been possible to observe the occurrence of sex-linked heterochromosomes in the meiosis of the males. As was demonstrated by D. Löve (15, 16, 17), Westergaard (32, 33), and Å. Löve (8), the meiotic divisions are not always the most appropriate stages for a detailed study of such chromosomes, since phenomena unrelated to sex determination may also result in heterobivalents. These authors found that mitotic divisions gave far more certain information on sex chromosome morphology than did meiotic divisions, and by these methods the identification of the heterochromosomes in the males of *Melandrium* and *Rumex* subgenus *Acetosella* was facilitated. A condition for such an identification is, of course, that many individuals of both sexes are investigated and that the fixation used must render the chromosomes fit for detailed morphological study.

In the material of *R. paucifolius* studied by the present writers, four chromosomes were found to be larger than the others in the root-tips of the female plants. In the male plants, however, only three such chromosomes could be discovered, although the total number of chromosomes was the same as in the females. By as close a comparison as was possible of the chromosomes of the male and female plants it was found that the fourth large chromosome of the female was replaced in the males by a small chromosome with median centromere, while the three large chromosomes of the males and the four large chromosomes of the females were identical in size and centromere position. The small chromosome of the male is a little smaller than any of the other chromosomes of the entire complement.

From these observations it seems safe to conclude that the four large chromosomes in the females and the three large chromosomes in the males probably are identical, and that these and the smallest chromosome without partner in the males are the sex chromosomes of *R. paucifolius*. In the following discussion the large chromosomes will be referred to as the *X*-chromosomes and the small one as the *Y*-chromosome, and they are marked as such in Figs. 1–2.

A sex mechanism based on three *X*-chromosomes and one *Y*-chromosome in the heterogametic sex and four *X*-chromosomes in the homogametic sex is known from *R. tenuifolius* (Wallr.) Löve of the *Acetosella* subgenus (7, 8), as well as from experimental autotetraploids of *Melandrium dioecum* (L.) D. Löve, (19, 20, 30, 31, 32, 33), and experimental autotetraploids of *R. angiocarpus* Murb. (Å. Löve, unpubl.). Since no genetical studies have yet been performed with *R. paucifolius*, it is, naturally, not possible to say with certainty how its sex determinants act, although the polyploid nature of the species and the number of its *X*-chromosomes must be taken as a strong indication that its sex mechanism does not follow the *Drosophila* scheme typical of the other dioecious taxa of the *Acetosa* subgenus. That scheme is assumed to prevent evolution of dioecious polyploids (cf. 2, 18, 34), while the *Melandrium* scheme followed by the *Acetosella* subgenus (8), allows evolution of dioecious polyploids up to a certain level.

The basic difference between the two main schemes of sex determination is the localization of the male and female determinants on the chromosomes. Plants evolving according to the *Drosophila–Acetosa* scheme have male genes only in the autosomes, female genes in the autosomes and in the *X*-chromosomes, but no significant sex genes in the *Y*-chromosomes. The sex of the individual is determined mainly by the balance between the number of autosome complements (*A*) and the *X*-chromosomes, so that a diploid plant with 2*A* and 2*X* (= 2 : 2 = 1.00) is a female, and a plant with 2*A* and *X* (= 2 : 1 = 2.00) is a male, irrespective of the occurrence of *Y*-chromosomes. Since individuals with *A* and *X* in proportions intermediate between 1.00 and 2.00 are intersexes, tetraploids with 4*A* and 3*X* (= 4 : 3 = 1.33) will be intersexual (2), so that polyploidy will result in gynodioecism rather than in dioecism. Also, as observed in some other sections of the subgenus *Acetosa* (Å. Löve (9) and unpubl.), species with this kind of localization of sex genes evolve from hermaphroditism through gynodioecism to dioecism at the diploid level.

While the *Y*-chromosome of plants developing their sex mechanism according to the *Drosophila–Acetosa* scheme is sexually inert, it is abundantly furnished with male determinants in biota of the *Melandrium–Acetosella* scheme. This latter group has female determinants in the autosomes and the *X*-chromosomes, but although male genes occur in some of the autosomes too, the decisive and strongly epistatic male determinants are found in the *Y*-chromosome. Since the male genes in the autosomes are weak, diploids with only one *X*-chromosome are female, while diploid plants with one *Y*-chromosome are male irrespective of how many *X*-chromosomes are present. It is known from experimental polyploids of *Melandrium* that one *Y* is strong enough to outweigh the effect of three or four *X*'s and four autosome complements, and in *Acetosella* artificial tetraploids, hexaploids, and octoploids with one *Y* are pure males (Å. Löve, unpubl.), as are such individuals of the three natural polyploid species of the subgenus (7, 8). Polyploids above the octoploid level still remain to be produced in this group, but the occurrence of weak intersexes in the panautoploids may indicate that the upper limit of the strength of the male determinants in the *Y*-chromosome has been reached at the octoploid level. This suggestion is also supported by the fact that only the octoploid species shows some tendency towards hermaphroditism. At the diploid level this kind of sex mechanism seems to go from hermaphroditism through androdioecism to dioecism.

The tetraploid state of *R. paucifolius* and the occurrence of three *X*-chromosomes in the males and four *X*-chromosomes in the females are good indications that its sex mechanism is based on the *Melandrium–Acetosella* scheme with strong male determinants in the *Y*-chromosome. The fact that androdioecism, i.e. a mixture of purely staminate and hermaphrodite individuals, is found to be fairly frequent in some populations, does not weaken this conclusion but merely indicates that the male genes in the autosomes may be almost as strong as are the female genes in the autosomes and

X-chromosomes together. In this phenomenon the sex mechanism of *R. paucifolius* and its unknown – and probably extinct – diploid ancestor, differs clearly from that of the subgenus *Acetosella*, most probably because it is younger or has developed more slowly and affected fewer of the male genes in the autosomes. The independence of both series is perhaps still better illustrated by the fact that while the *Y*-chromosome of *Acetosella* is the largest chromosome of the complement and the *X* is only slightly larger than the autosomes, the *Y*-chromosome of *R. paucifolius* is the smallest chromosome and the *X*-chromosomes are almost twice as large as the autosomes. Also, the morphological characters of *R. paucifolius* leave no doubt as to its distinctness from the subgenus *Acetosella*, and its grouping into the subgenus *Acetosa* seems to be well founded.

Before discussing further the sectional classification of *R. paucifolius* within the subgenus *Acetosa*, a short review of the modern classification of the genus *Rumex* is of interest. It was pointed out by Rechinger (21) that the genus could be divided into three distinct subgenera, *Rumex* (= *Lapathum*), *Acetosella*, and *Acetosa*. Specializing on the first subgenus, Rechinger (21, 22) included in it the three sections *Rumex* (= *Simplices* Rech.f.), *Axillares*, and *Platypodium*, but left the other subgenera undivided.

It was demonstrated by Å. Löve (8, 10) that the classification by Rechinger (21) is well founded from the point of view of cytotaxonomy, since the subgenera proposed by him were not only morphologically distinct and separated by a complete barrier of incompatibility, but also cytologically very dissimilar due to differences in size and basic number of their chromosomes and the occurrence or lack of polyploidy. Later, Å. Löve (11, 12) also pointed out that the subgenera were in fact so distinct as to warrant their separation as good genera. Within the subgenus *Rumex* the two sections *Rumex* and *Axillares* are characterized by the basic number $x = 10$, the chromosomes are small with mainly median centromeres, but although polyploidy and hybridization are common in the section *Rumex*, they are rare in the section *Axillares* (26). The section *Platypodium*, which includes only one variable species (cf. 22, 25), has larger chromosomes, its basic number is $x = 8$ and polyploidy is absent as far as is known. It was separated as a distinct subgenus by Å. Löve (11) and, independently, by Rechinger (25). The subgenus *Acetosella* has again somewhat larger chromosomes with subterminal, submedian, and median centromeres, the basic number is $x = 7$, and three of the species form a polyploid series from the tetraploid to the octoploid level (Å. Löve 7, 8, 12 and unpubl.). The subgenus *Acetosa*, however, is morphologically as well as cytologically considerably more variable than all the other subgenera; its chromosomes are usually larger and it has several basic numbers. And until the discovery of the tetraploidy of *R. paucifolius*, only two polyploids were known from within this huge subgenus.

The subdivision of the subgenus *Acetosa* was commenced by Å. Löve (10), who based his classification on cytological as well as morphological criteria. Four sections were proposed: *Acetosa* (= *Euacetosae* Löve) for the dioecious

species with $2n = 14♀, 15♂$ chromosomes; *Vesicarii* for hermaphrodite annuals with $2n = 18$ chromosomes; *Hastati* for a gynodioecious group with $2n = 18$ and 36 chromosomes; and *Scutati* for perennial hermaphrodite plants with $2n = 20$ and 40 chromosomes. This classification was adopted by Rechinger (24), who added the dioecious and annual section *Insectivalvis* with $2n = 18$ chromosomes (Å. Löve, unpubl.), and later, Rechinger (25) added a new and large section *Afroacetosae* with hermaphrodite, polygamous, monoecious, and dioecious species, the cytology of which remains unknown. This section is placed between *Acetosa* and *Insectivalvis* and seems to be closely related to the former.

As to the classification of the dioecious endemic North American species *R. hastatulus* and *R. paucifolius* in this system of sections, it was suggested by Å. Löve (11) that both might belong to the section *Acetosa*. However, since Smith and Smith (28) had demonstrated that *R. hastatulus* has only the chromosome number $2n = 8♀, 9♂$ but otherwise the chromosome size and sex chromosome complex typical of *Acetosa*, it was suggested that the American endemics might rather form a separate subsection of section *Acetosa*, named *Americanae*. This view is strongly substantiated by the more detailed studies by Smith (27) on *R. hastatulus*, so that there is little doubt as to the correctness of dividing the section *Acetosa* into two subsections, one, subsection *Acetosa*, including all the Eurasiatic and arctic–subarctic circumpolar species related to *R. Acetosa*, and the other including *R. hastatulus* alone. This latter group should be named:

Rumex subgenus *Acetosa* section *Acetosa* subsection *Americanae* Löve & Sarkar, subsect. nova: Flores dioici. Folia basalia divergentibus hastato-sagittata. Numerus cardinalis chromosomaton $x = 4, 5$. Typus: *Rumex hastatulus* Baldw.

Although the present observations on *R. paucifolius* and its cytology do not contradict its classification in the subgenus *Acetosa*, it is evident that its close relationship to the other dioecious species of the group is not only doubtful but also highly improbable. The evolution of this species has followed an opposite line to that of section *Acetosa* from the very beginning of its dioecism, as shown by the differences in morphology and constitution of its sex chromosomes; the different basic number and the size and morphology of the autosomes also support this view. Therefore, the present writers feel confident that *R. paucifolius* is sufficiently distinct from all other groups of subgenus *Acetosa* to constitute a section of its own. For this new section the writers propose the name:

Rumex subgenus *Acetosa* section *Paucifoliae* Löve & Sarkar, sect. nov.: Flores dioici vel androdioici. Radix crassa. Folia basalia lanceolata vel ovato-lanceolata, nunquam hastata vel auriculata. Numerus cardinalis chromosomaton $x = 7$. Typus: *Rumex paucifolius* Nutting.

As to the relationship of the new section to the six previously described sections of the subgenus *Acetosa*, the former classification of the species *R. paucifolius* close to the other dioecious *Rumex* might suggest that it could

TABLE I

TAXONOMICAL SUBDIVISIONS OF *Rumex*

Taxa	Sexual condition	Cytology
Genus *Rumex* L.		
Subgenus *Rumex*		$x = 10$
Section *Rumex*	Hermaphrodite	$2n = 20 - 200$
Section *Axillares* Rech.f.	Hermaphrodite	$2n = 20 - 60$
Subgenus *Platypodium* (Willd.) Löve	Hermaphrodite	$x = 8$; $2n = 16$
Subgenus *Acetosa* (Campd.) Rech.f.		$x = 4, 5, 7, 8, 9, 10$
Section *Acetosa*		
Subsection *Acetosa*	Dioecious	$2n = 14♀, 15♂$
Subsection *Americanae* Löve & Sarkar	Dioecious	$2n = 8♀, 9♂$
Section *Afroacetosae* Rech.f.		
Subsection *Abyssinici* Rech.f.	Polygamous – hermaphrodite	Unknown
Subsection *Capensis* Rech.f.	Monoecious – polygamodioecious	Unknown
Subsection *Sagittati* Rech.f.	Dioecious	Unknown
Section *Insectivalvis* Rech.f.	Dioecious	$2n = 18$
Section *Vesicarii* Löve	Hermaphrodite	$2n = 18$
Section *Hastati* Löve	Gynodioecious	$2n = 18, 36$
Section *Scutati* Löve	Hermaphrodite	$2n = 20, 40$
Section *Paucifoliae* Löve & Sarkar	Dioecious	$2n = 28$
Subgenus *Acetosella* (Meisn.) Rech.f.	Dioecious	$x = 7$; $2n = 14, 28, 42, 56$

be placed close to the section *Acetosa*. Because of its cytological distinctness, however, the present writers are of the opinion that it should be placed as far from the other dioecious *Acetosae* as possible, though within the same subgenus. This is shown in Table I, which also reviews the classification of the other subgroups of *Rumex*, with the exception of the subsections of subgenus *Rumex*.

It has been pointed out previously by Á. Löve (8, 10, 12), Rechinger (23, 24, 25), Lousley (6), and Datta (3) that the genus *Rumex* is an unusually suitable taxon for combined morphological and cytogenetical studies of evolutionary processes. The present paper once more substantiates this statement. Morphological studies alone could not definitely solve the problem of the relationship of *R. paucifolius* to other dioecious *Rumex*, and there was even doubt as to the accuracy of placing it within the subgenus *Acetosa*. The present studies reveal that the species is cytologically distinct from other dioecious taxa of the group and constitutes a section of its own. It is apparently a tetraploid relict of a primitive group, which has not taken part in the further evolution of the other taxa of this variable genus.

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THE NATIVE PLANTS OF CHURCHILL, MANITOBA, CANADA[1]

By J. C. Ritchie[2]

Abstract

The object of the paper is to provide as complete an account as is possible of the native vascular plants of a circumscribed area near Churchill, Manitoba, on the west coast of Hudson Bay. Preceded by an account of earlier major collections and reports, brief surveys of the topographical, geological, and climatic features of the region are presented. Associated with the four main topographical types there are discrete groups of plant communities; they are described in general, qualitative terms. An annotated account of the 270 entities of native vascular plants found in the area is submitted, in which autecological notes and data of distribution are appended to the name of each species. There are seven additions to the known flora of Manitoba; one new variety is described. The geographical affinities of the flora are examined, in broad outline, and it is shown that the flora consists of 53% arctic and subarctic plants, 45.5% boreal and 1.5% cosmopolitan species. Six species have amphi-Atlantic areas, and nine belong to that group of plants which have their main areas in North America with outlying stations in Northwest Europe.

I. Introduction

By its ease of access and its central position on the periphery of the North American Arctic, Churchill has long been a mecca for botanists, both resident and transient. Consequently it probably ranks as the most completely studied area in the Canadian Subarctic. Yet, the most comprehensive and accurate reports which are available in no way provide a complete record of the flora and vegetation of this vicinity. For this reason, and because of the considerable ecological and phytogeographical interest of the area, the present paper attempts to present a complete account of the native vascular plants of the area, preceded by brief treatments of the topography, geology, climate, and ecology, and followed by an examination of the geographical affinities of the flora. The whole is based in part on the writer's field investigations during the summer of 1954, and in part, as will be indicated, on the existing literature and plant collections from the area. In the interests of accuracy, the investigations which are described below have been confined to a particular area (Fig. 1), and any localities for plant records which do not lie within this area have been excluded from the account.

The first plant records specifically from Churchill are those of Robert Bell, reported in 1880 (Bell (5)). This work was followed by the memorable explorations of J. B. Tyrrell in 1893–4, so exhaustively reported and annotated (Tyrrell (66)) and including a list of plants collected at Churchill. In 1910 J. M. Macoun collected plants at Churchill but no detailed publication was made dealing with the area in particular. A report on the collections made by the members of the Fifth Thule Expedition 1921–24 was provided by Grøntved (21) and this includes 65 species of vascular plants collected at Churchill. In 1929 Frits Johansen collected plants at Churchill (and elsewhere in the

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region) and two reports were published of this work – a descriptive account (Johansen (31)) and a list of the plants which were collected (Störmer (63)). Including the earlier work of Bell (5), Tyrrell (66), and Macoun, Johansen (31) cites 112 as the total number of species of vascular plants known from Churchill. It is of interest here to note that Johansen (31) discusses the claim of Macoun (40) that there is no arctic element in the flora of Churchill and concludes that "the vegetation is a mixture of subarctic and arctic species, about evenly divided as to their number".

In 1930 G. Gardner included Churchill in his botanical investigations along the western shore of Hudson Bay, and an account of the plants he recorded is available (Gardner (19)). In the same year (1930) A. E. Porsild and V. W. Jackson made collections (separately) from the environs of Churchill; neither has been recorded *in toto* in print. W. C. Güssow made a small collection in the same area in 1932 and his report (Güssow (22)) includes records from Churchill. In 1934 and 1936 Dr. Nicholas Polunin made collections from the region and M. Duman and his co-workers (A. Dutilly, H. O'Neill, and E. Lepage) made various collections between 1938 and 1946.

In 1939 A. H. R. Buller made a small collection of vascular plants from the immediate vicinity of Churchill. The perennial activities of Mrs. Eva Beckett of Churchill have yielded a wealth of botanical information during the last 15 years, largely in the form of collections which are found in various herbaria in North America; also she has made a contribution to the published record of the flora of the region (Beckett (4)). Further extensive gatherings of plants were made by Dr. Polunin in 1947.

In his "List of the Flowering Plants, Ferns, Club Mosses, Mosses and Liverworts of Manitoba" Lowe (38) cites Churchill as the locality for some 92 species of vascular plants, based, apparently, on the collections of Jackson and Buller (mentioned above) and that of Mrs. A. Simpson in 1942 (the last is found in the herbarium of the Natural History Museum, Winnipeg). Unfortunately Lowe's (38) account specifies neither collector nor exsiccate number for particular species and it has been found difficult to confirm certain of the records.

In recent years, under the auspices of the Defence Research Board of Canada, collections of plants have been made from the army base at Fort Churchill, a few miles east of Churchill; these have been reported on by the main collectors Gillett (20) and Beckel (3). Unfortunately the latter account is of little botanical value as the list of species, which includes collections from widely separated regions of Hudson Bay, gives no indication of the geographical locality of the specimens. And of course neither account is freely accessible, the former being available only on short loan and the latter being in very limited supply.

The investigations of "biotic communities" by Shelford and Twomey (61) and McClure (39) at Churchill contain little new information of botanical interest, and their floristic records are somewhat meagre and, in some instances, inaccurate.

Dr. J. W. Thomson has provided an annotated list of the lichens of Churchill (Thomson (65)) based on his field work there in 1950.

It is realized that the above review is incomplete as it excludes certain smaller and unreported collections which have been made at Churchill.

II. Geology and Climate

(a) Geology

One of the earliest accounts of the geology of Churchill, that of Tyrrell (66), remains the most authoritative and informative which is available, although it has been briefly reiterated, with a little new information, by Williams (69, 70). The earliest formal descriptions, by Bell (5, 6) provide useful details to supplement Tyrrell's comprehensive treatment, and Birket-Smith (7) has given a general account of the geology of the Barren Grounds; Churchill lies at the southeast apex of this region. The following brief account is based almost entirely on Tyrrell (66), and is presented merely to align the geological evidence with the botanical problems of the circumscribed area of study.

On the west side of the River Churchill, and along the axis of Cape Merry (see Fig. 1) extending eastwards along the coast, there are rocky ridges which seldom exceed 35 meters above sea level. These are composed of "....a greenish-gray even-grained, false-bedded, felspathic arkose sandstone .... often cut by many irregular veins of dull white quartz." (Tyrrell (66)). Bell (5) first coined the term 'Churchill quartzite' for this formation, and it has been so described in subsequent literature; it is used freely in this paper. Tyrrell (66) ascribes this outcrop to the Cambrian period. He also records

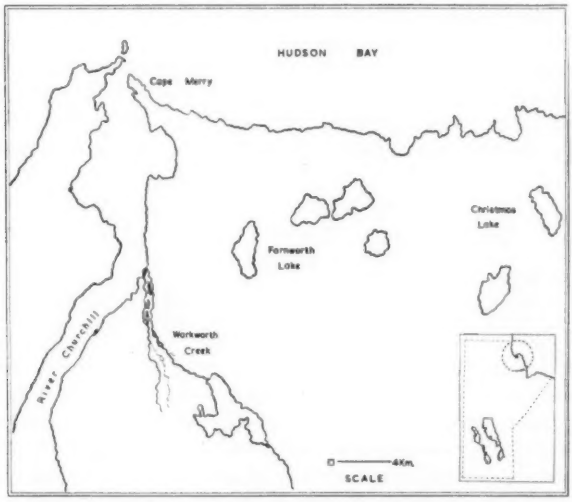

FIG. 1. An outline map showing the area of study with which this report is concerned. The inset map of the province of Manitoba indicates the position of this area on the west coast of Hudson Bay.

his observation of "a small outlier of an unaltered Cambro–Silurian limestone. . . ." found on the west side of the Churchill river. Scattered along the river estuary zone are ". . . . masses of white limestone," (Tyrrell (66)) which is Silurian and has been transported from proximate bedrock by ice action.

By far the greater surface area is covered by till of Pleistocene age, consisting of silt, calcareous clay and pebbles, boulders, and rock flour. The land which is covered by this till is flat or gently sloping, forming the vast plains of much of Northern Manitoba and Keewatin, broken only by outcrop ridges, eskers, moraines, raised beaches, and shore lines.

An account of the recent geological history is of relevance in an examination of the contemporary flora and vegetation of the area, and the following description is culled from the works of Tyrrell (66), Antevs (1), Birket-Smith (7), Johnston (33), and Williams (69). It should be noted that only the points which are strictly relevant will be abstracted from the mass of interesting data on the postglacial history of this part of Canada, to which the above citations, along with others, refer.

Of the three main glaciers which covered much of Canada during the last glaciation, that which had its centre of origin in Keewatin – the Keewatin Glacier of Tyrrell (66) – was the only one which affected directly the area of this study. Somewhat exceptionally, the rocky ridges at Churchill are rounded and striated in a manner which has led Tyrrell (66) to postulate that the evidences of a westward glaciation "were probably caused by a more or less local glacier moving westward from a névé near the shore, ..., possibly centering in the vicinity of Cape Churchill, thirty miles east of the mouth of Churchill River". But the main direction of the ice 'advance' was from the North and the entire area of our study was covered by the continental Keewatin Glacier. As the ice sheet waned, it formed the northeast boundary of the glacial Lake Agassiz which covered most of Manitoba, and the initial drainage of this lake into Hudson Bay must have taken place along the present-day courses of the Little Churchill and Churchill Rivers. Contemporary with, and persisting after the diminution of the Keewatin icecap, the level of the sea in this area rose, owing to the tilting of the land by the weight of ice. Many authors have discussed this event, particularly Bell (5), Tyrrell (66), Birket-Smith (7), Potter (47), Williams (69), Moir (41), and Boivin (13). The clearest evidence of this postglacial submergence is the existence of extensive shore lines at considerable distances westward from the present Hudson Bay west coast line. The most conspicuous beach lies 85 km. west southwest of Churchill and extends south to the region west of James Bay, and discontinuously north into Keewatin. In this and other beaches many marine fossils have been found. The concensus of opinion is that, immediately following the 'retreat' of the ice from the region, the whole of the coastal fringe of Hudson Bay was inundated, to distances varying from 75 to 200 km. The present topography evinces this submergence by the low coastal plain separated from the higher inland plateau by the old marine

beaches. The rising of the land effected a retreat of the sea from the coastal plain. From marine deposits inland from Churchill, and elsewhere in the region, it is clear that the Late-Glacial sea must have been at a level approximately 150 m. above the present sea level – the 500 ft. contour coincides approximately with the maximum postglacial extension of Hudson Bay. Antevs (1) suggested 9000 years as the approximate age of the Post-Glacial period in central North America, and it seems reasonable to assume that the Late-Glacial sea had at least submerged the area of this investigation approximately 10,000 years ago. The exact duration of the Late-Glacial sea is not certain, and Bell (6) has indicated that it was certainly higher than its present level not more than 1000 years ago; in this estimation the disposition of ancient eskimo camps in relation to the present shore line is the evidence cited. But from a botanical viewpoint the recent work of Potzger and Courtemanche (48) is of greatest interest and relevance; they have dated the earliest deposits of organic material on the till under a bog at James Bay, Quebec, and the age determination which carbon-14 analysis has yielded is 2350 ($\pm$200) years. No such dating is yet available for Churchill, but it seems reasonable to suggest that the age of the peat must be of the same order as that of the James Bay station.

The only study of peat stratigraphy in this area is by Johnson (32), whose very preliminary investigations have yielded only the most general and tentative of conclusions. From samples of peat from the area studied Johnson (32) suggests that the first vegetation to colonize the till was a sedge-dominated type, followed by heath, birch scrub, and spruce forest. He ascribes the subsequent extinction of continuous forest in the large 'barren' about 40 km. south of Churchill to the "acid sphagnum-bog conditions". He notes a "sphagnum retrogression" to the "lichen–ericaceous heath" which covers much of the terrain south of Churchill. However, this is scarcely compatible with the fact that there are vast tracts of peat, particularly in the zone immediately south of Churchill, which are spruce dominated with a ground flora largely dominated by various *Sphagnum* and *Cladonia* spp. In many parts of the treeless region which Johnson (32) describes there is evidence of forest burning, and this factor would appear to be worthy of investigation as the possible cause of local extinction of the spruce cover; Lewis and Dowding (35) have indicated the importance of this factor in the retrogression of peat vegetation in central Alberta.

(b) Climate

The task of elucidating those factors of climate which are operative in determining the survival and performance of plants in arctic regions has scarcely been begun. And at Churchill only the major aspects of the role of climatic factors are apparent. The following table provides a comparison of temperature data from boreal (The Pas), subarctic (Churchill), and arctic (Arctic Bay) stations.

TABLE I

MONTHLY MEANS OF THE AVERAGE DAILY TEMPERATURE (°F.)

	The Pas, Man.		Churchill, Man.		Arctic Bay, N. Baffin Is.	
	Max.	Min.	Max.	Min.	Max.	Min.
Jan.	−8.7	−18.1	−19.0	−26.7	−19.6	−26.7
June	59.2	48.2	42.6	33.6	35.5	29.5
July	64.6	53.8	53.7	42.8	43.3	35.7
Aug.	60.6	49.6	52.4	42.6	40.8	34.9
Sept.	48.9	37.8	41.8	34.5	30.0	25.8
Dec.	0.6	−7.8	−11.0	−18.9	−16.8	−23.2

The climate of Churchill is characterized by higher summer temperatures, a longer season suitable for plant growth and greater day length than truly arctic stations, such as Arctic Bay. Polunin (43) has given data of temperature from Chesterfield Inlet (63°20′N., 90°42′W.) which show clearly the remarkable increase in severity of the climate between Churchill and this station, a distance of approximately 650 km.

In the classification by Sanderson (60), Churchill is included in the cool microthermal (c_1') zone with an evapotranspiration value of 35 cm., and by the criterion of moisture index in the moist subhumid (c_2') region.

It lies in that zone which marks the northern limit of microphanerophytic growth. However, along this transition or 'tree line' local variations in edaphic factors appear to be responsible for greater or lesser extensions of the taiga into the true tundra and the ecological problems involved in this have been explored by only a few workers. The coincidence of the southern limit of permafrost (map in Jenness (30)) with the southern area of this transition suggests, as Jenness (30) points out, that this might well be the primary factor which inhibits tree growth in many areas. It is possible that, within the wider limits directly imposed by climatic factors, such edaphic factors as the presence of permafrost might determine the precise configuration of the tree line.

By climatic criteria Churchill has been included in the Arctic. Polunin (44 and 45) has provided maps on which the Nordenskiöld line has been plotted, and Churchill is situated immediately within this boundary, although Polunin's definition of the Arctic based on both biological and climatic data excludes it by a short distance. It would appear that the vegetation at Churchill would conform accurately to Rousseau's (59) 'zone hemiarctique'. This is defined as "... une association d'habitats franchement arctiques et d'habitats franchement subarctique". In the comparable terminology of Hare (24), the vegetation represents the forest-tundra ecotone between the true arctic tundra and the subarctic open boreal forest (taiga).

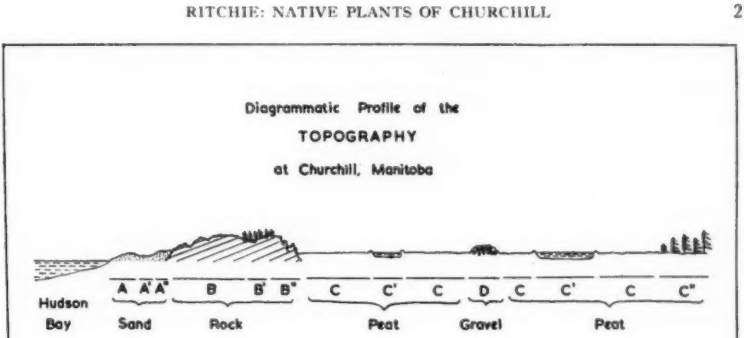

FIG. 2. A highly diagrammatic representation of the main features of topography in the region. The associated vegetation types are: A, the foreshore zone; A′, the damp dune hollows; A″, the stable dunes; B, the heath type; B′, the spruce scrub; B″, the ledge communities; C, low peat areas; C′, pools and lakes; C″, the spruce forest over peat; and D, the communities of gravel ridges.

III. The Vegetation of the Area

There are four major physiographic formations at Churchill, associated with which there are discrete aggregations of plants. As is illustrated in Fig. 2, sand, rock, organic material, and gravel comprise the salient types of the region, excluding the estuary flats and shores. By dint of their particular edaphic properties these substrata bear different vegetational types which will be described separately in the discourse which follows.

(a) Plant Communities on Sand Deposits

The areas of sand are coastal and those which were studied in detail abut upon the outcrop ridge of the north shore of Cape Merry. As Fig. 2 indicates, the sand area is made up of four zones. Immediately above high-tide level there is a low, flat region, often with scattered limestone pebbles and gravel, which extends for 10–20 meters inland and might be described as the *foreshore zone*. The plants of this zone are in part halophytes, in part strand plants, and the following list was compiled from a study of the foreshore community at Fort Churchill, Cape Merry (the standard frequency symbols are used).

Honkenya peploides	la	*Rumex occidentalis*	lf
Atriplex patula	f	*Hippuris tetraphylla*	o
Carex maritima	f	*Tripleurospermum ambiguum*	o
Cochlearia arctica	f	*Plantago borealis*	o
Puccinellia airoides	f	*Trisetum spicatum*	o
Argentina pacifica	lf	*Cytorhyncha cymbalaria*	o

Inland, the sand is formed in low ridges and dunes – badly disturbed by military vehicles – in which conditions of drainage are free and the water

table is low. These *open dunes* are characterized by rhizomatous perennials and deep-rooting annuals. The following list indicates the general physiognomy of the vegetation:

Elymus mollis	a, ld	*Arabis arenicola*	o
Festuca brachyphylla	f, la	*Braya humilis*	o
Arctous rubra	f, la	*Erigeron elatus*	o
Castilleja raupii	f	*Gentianella propinqua*	o
Potentilla multifida	f	*Lesquerella arctica*	o
P. pulchella	f	*Potentilla pensylvanica*	o
Trisetum spicatum	f	*Solidago multiradiata*	o
Androsace septentrionalis	o, lf	*Tortula ruralis*	f
Achillea millefolium	o	*Catoscopium nigricum*	o

Between the open dunes and the outcrop ridge are higher *stable dunes*, with a continuous cover of vegetation. The following list is typical of this zone:

Arctous rubra	a, ld	*Elymus mollis*	o
Dryas integrifolia	a, ld	*Empetrum hermaphroditum*	o
Achillea borealis	f	*Festuca brachyphylla*	o
Carex glacialis	f	*Potentilla nivea*	o
Castilleja raupii	f	*P. pensylvanica*	o
Chamaenerion angustifolium	f	*Pyrola grandiflora*	o
Hedysarum mackenziei	f	*Rhinanthus borealis*	o
Salix arctophila	f	*Vaccinium uliginosum*	o
S. cordifolia	f	*Alectoria jubata*	lf
S. reticulata	f	*Cetraria nivalis*	f
Shepherdia canadensis	f	*C. islandica*	o
Chamaenerion latifolium	o	*Cladonia rangiferina*	o
Draba hirta	o	*Peltigera canina*	o

Locally, there are flat areas of sand in sheltered hollows where the water table is near the surface in early summer and where edaphic conditions are suitable for plants of wet, eutrophic preferences. Floristically and edaphically these habitats are similar to the dune 'slacks' or wet dune valleys of Tansley (64). At Churchill these areas occur as small patches, usually about 10×30 m. The following list of plants was recorded from one of these areas near Fort Churchill:

Achillea borealis	f	*Betula glandulosa*	o
Bistorta vivipara	f	*Epilobium palustre*	o
Carex vaginata	f	*Erigeron humilis*	o
Castilleja raupii	f	*Pinguicula vulgaris*	o
Parnassia multiseta	lf	*Platanthera hyperborea*	o
Primula egaliksensis	f	*Ribes oxyacanthoides*	o
P. stricta	f	*Salix brachycarpa*	o
Rubus acaulis	f	*Solidago multiradiata*	o
Arctous rubra	o	*Saxifraga aizoides*	o

Tofieldia pusilla	o	*Tomenthypnum nitens*	f
Rumex occidentalis	r	*Mnium affine*	o
Aulacomium palustre	f	*Drepanocladus aduncus*	o
Hypnum revolutum	f		

In those areas where sand has blown on to the rocky ridge, filling cracks and hollows, there are occasional sandy pools which show a constant zonation of plants. These pools seldom exceed three meters in diameter. In the shallow water the dominant species are usually *Potamogeton pectinatus*, *Hippuris vulgaris*, and less commonly *H. tetraphylla*. Immediately surrounding the water, in wet sand, there are discrete zones, usually of *Juncus arcticus* and *Equisetum variegatum*.

In local stations in the sand/rock ecotone, *Picea glauca* occurs in sheltered, stable sand, and here *Betula glandulosa* occurs, often reaching a height of one to two meters.

(b) Plant Communities on the Outcrop Ridge

By the diversity of substrata on the quartzite ridges there are many local plant facies, the floristic composition and structure of which are influenced by the orientation of the rock surfaces, drainage, shelter from the wind, humus accumulation, and other factors. Only the major community types will be described here.

On the exposed, flat tops of the ridges, trees are absent, or where present they scarcely exceed ½–1 meter in height, more commonly being prostrate and stunted. Here an essentially *heath-type vegetation* prevails, that is, a community in which the dominant plants are ericaceous or ericoid shrubs. A conspicuous component of this heath is the lichen cover, chiefly represented by species of *Cladonia*, *Cetraria*, *Alectoria*, and *Parmelia*. The following list of plants purports to indicate only the general floristic features; for an elucidation of the various ecological problems, particularly concerning the interrelationships of the dominants, more critical study is needed:

Arctous alpina	a, ld	*D. alpina*	o
Dryas integrifolia	a, ld	*Luzula frigida*	o
Empetrum hermaphroditum	a, ld	*L. parviflora*	o
Vaccinium uliginosum	f, la	*Poa pratensis*	o
V. vitis-idaea	f, la	*P. alpina*	o
Salix reticulata	f, la	*Cetraria nivalis*	a
Astragalus alpinus	f	*C. islandica*	f
Loiseleuria procumbens	f	*Cladonia alpestris*	f
Pedicularis lapponica	f	*C. rangiferina*	f
Rhododendron lapponicum	lf	*Alectoria ochroleuca*	f
Bistorta vivipara	o	*Peltigera canina*	o
Draba nivalis	o	*Sphaerophorus globosus*	o

These plants are typical of humous substrata, many perennate by underground rhizomes or rootstocks, and several appear to be mycorrhizal.

In *ledges, crevices, and sheltered niches* there is a varied assortment of plants, all species which are confined to areas with protection from wind and frost. Such plants, found in the cliffs and boulder screes of the southern margin of the ridges, are as follows:

Botrychium lunaria (uncommon)
Campanula uniflora (local)
Cystopteris dickieana
C. fragilis
Draba cinerea
D. lactea
D. nivalis
Dryopteris disjuncta (rare)
Juniperus communis
Minuartia rubella
Pyrola grandiflora
Ramischia secunda
Ribes hudsonianum
Salix arctophila
S. desertorum
S. reticulata
Saxifraga caespitosa
S. tricuspidata

In hollows and depressions in the ridge, where drainage is impeded, standing water is common, forming *lakes, pools, and tarns.* The vegetation of these aquatic habitats is varied and would require a more detailed study than is possible here, but the following list will indicate the range and diversity of species aggregates which are found:

Submerged or floating
Callitriche hermaphroditica
Hippuris tetraphylla
H. vulgaris
Myriophyllum exalbescens
Potamogeton filiforme
Sparganium angustifolium

Marginal or partly submerged
Cicuta mackenzieana
Eleocharis palustris
Eriophorum angustifolium
E. callitrix
Juncus balticus
Senecio congestus var. *palustris*
Sparganium hyperboreum

The fourth community on the ridge which merits description is that associated with the *spruce scrub.* The trees seldom exceed 4 meters, often being stunted and with little growth on the sides facing the prevailing wind, and they are found in slight depressions where soil accumulation is considerable and protection from the wind is greatest. In the more shaded parts of the ground layer the following plants are found:

Bartsia alpina	f	*Parnassia kotzebuei*	o
Geocaulon lividum	lf	*P. multiseta*	o
Pedicularis lapponicus	f	*Pyrola minor*	o
Platanthera obtusata	f	*Rhinanthus borealis*	o
Orchis rotundifolia	f	*Corallorhiza trifida*	r
Rubus acaulis	f	*Drepanocladus aduncus*	f
R. chamaemorus	lf	*Hylocomium alaskanum*	f
Smilacina trifolia	f	*Mnium affine*	f
Tofieldia pusilla	lf	*Tomenthypnum nitens*	f
Moneses uniflora	o	*Ditrichum flexicaule*	o

In open places the following species assume dominance, usually where the humous soil of the shaded wood is replaced by a damper soil with underlying clay or gravel:

Astragalus alpinus	f	*Calamagrostis canadensis*	o
Carex scirpoidea	f	*Carex capitata*	o
Castilleja raupii	lf	*Cerastium alpinum*	o
Cypripedium passerinum	lf	*Elymus mollis*	o
Juncus castaneus	lf	*Poa alpina*	o
Arctagrostis latifolia	o	*Trichophorum caespitosum*	o

(c) Plant Communities of the Plain

As has been indicated, the extensive area occupied by this terrain consists largely of glacial till underlying a layer of peat. This, together with the occurrence of an impervious layer of permanently frozen subsoil – the permafrost or more technically, pergelisol of Bryan (14) – is inimical to free drainage and favours the accumulation of surface water as pools, and small lakes. This resulting mosaic of pools and bogs comprises much of the plains region. There are three main vegetation types but the transitions between them are not abrupt and many intermediate types exist. The *marginal and aquatic vegetation* of lakes and pools is varied yet discrete. The more common aquatic species are *Comarum palustre*, *Equisetum fluviatile*, *Hippuris vulgaris*, and *Menyanthes trifoliata*. Pools and lakes are characterized by a raised peripheral zone, 0.5–1 meter high; Raup (50) and Lewis, Dowding, and Moss (36), have described apparently similar phenomena in the Mackenzie District and Alberta respectively. Raup (50) accounts for the ridge formation in terms of the differential accumulation of peat by *Scirpus validus* and *Typha latifolia* and the recent lowering of the water level exposing these ridges. It is doubtful if this explanation can be applied successfully to the area of this study as there is no evidence for a zonal dispersion of plants which form unusually large amounts of peat. The phenomenon described by Lewis, Dowding, and Moss (36) seems to be related in part to the peculair orientation of the superficial lateral roots of trees of *Larix* and in part "... to the fact that the water level of the quaking bog has been lowered ...". It appears that the ridge phenomenon at Churchill is explicable in terms of ice action (cf. Raup (51), p. 167); it seems likely that, at least for small bodies of water, the ridges are caused by the slight annual expansion and hence radial pressure of the ice, effecting a raising of the marginal peat. The writer finds it difficult to apply Tyrrell's (67) explanation that they are caused by wind controlled ice movement, at least in the case of small lakes of less than 50 meters in width. The conditions of improved drainage which prevail on these ridges are responsible for the presence of such characteristic plants as *Betula glandulosa* and *Salix myrtillifolia*. The plants on and in the region of this ridge are listed below:

Betula glandulosa	ld	*Carex aquatilis*	lf
Salix myrtillifolia	a	*Equisetum fluviatile*	f
S. calcicola	a	*Eriophorum scheuchzeri*	f

Menyanthes trifoliata	f	*Galium brandegei*	r
Salix cordifolia	f	*Viola palustris*	r
S. desertorum	f		
Stellaria calycantha	f	*Aulacomnium palustre*	a
S. ciliatosepala	f	*Calliergon stamineum*	f
Carex rotundata	o	*Drepanocladus aduncus*	f
C. miliaris	o, lf	*Sphagnum rubellum*	f

The greater area of the plains is occupied by *peat bog*, corresponding with the 'low wet tundra' of Shelford and Twomey (61) and the 'sedge meadow' of Gillett (20). This is a floristically diverse formation. As an example of one of the several bog facies which are found, the following were recorded in a small bog near Farnworth Lake:

Andromeda polifolia	f	*Trichophorum caespitosum*	f
Carex gynocrates	f	*Triglochin maritima*	f
C. rariflora	f	*Carex atrofusca*	o
Ledum groenlandicum	f, la	*C. vaginata*	o
Myrica gale	f, la	*Cardamine pratensis*	o
Oxycoccus microcarpus	f	*Kalmia polifolia*	o
Pedicularis sudetica	f	*Pedicularis flammea*	o
Rubus chamaemorus	f	*Rhododendron lapponicum*	o, lf
Saxifraga hirculus	f	*Trichophorum alpinum*	o
Stellaria calycantha	f	*Triglochin palustris*	o

Locally, and continuously in the southern part of the area of study, the peat is tree-covered, *Picea mariana* being the dominant. The *spruce forest zone* is confined to areas of the plains where drainage is slightly improved. Associated with the dominant is a ground layer which yielded the following list of species in a particular locality:

Cladonia alpestris	d	*Lycopodium annotinum*	o
Ledum groenlandicum	a, lf	*Peltigera aphthosa*	o
Rubus chamaemorus	f	*Platanthera hyperborea*	o
Corallorhiza trifida	o	*Vaccinium uliginosum*	o
Kalmia polifolia	o		

In this community, on slightly elevated ridges, lichen polygons are common features of the ground vegetation. This phenomenon, involving only the dominant *Cladonia alpestris*, has been described and explained by Rousseau (58). In areas where small patches of spruce trees occur a community of species common to both the preceding lists (the last and the penultimate) is found. *Larix laricina* occurs throughout the area, never abundant, usually confined to the wet peat of pool margins and hollows.

(d) Plant Communities of the Gravel Ridges

On the exposed summits of the gravel ridges is a lichen–heath vegetation, of which the following list is typical:

Dryas integrifolia	d	*Draba incana*	o
Bistorta vivipara	f	*Erigeron elatus*	o
Hierochloe odorata	f	*Linum lepagii*	o
Saxifraga oppositifolia (confined to open habitats)	f	*Taraxacum lacerum*	o
Achillea borealis	o		

On the flanks of certain ridges, where drainage is impeded, there is a rich sedge-meadow community. The following list was recorded near Christmas Lake, at the eastern boundary of the area, where the substratum was an eutrophic shallow peat over gravel:

Carex rariflora	f, la	*Triglochin maritima*	f
Arctagrostis latifolia	f	*Oxycoccus microcarpus*	o
Carex atrofusca	f	*Petasites sagittatus*	o
C. vaginata	f	*Primula egaliksensis*	o
Epilobium palustre	f	*Poa arctica*	o
Pedicularis flammea	f	*Coptidium lapponicum*	o
Saxifraga hirculus	f		

Twin Lake Hill, in the southeast part of the area (Fig. 1), is a large, roughly rhomboidal gravel deposit, over 100 meters high, 5 km. long, with a flat top and steeply sloping flanks on the southern side. The exact geological origin of this atypical formation is uncertain, but it appears to be a fluvioglacial deposit. It is of botanical interest since it bears a vegetation, on the plateau, which is more typical of the taiga than of the forest-tundra of the rest of the area. *Picea alba*, *P. mariana*, and *Populus balsamifera* comprise the tree-cover, while the ground vegetation is locally dominated by *Arctous rubra*, *Juniperus communis*, *Vaccinium vitis-idaea*, *V. uliginosum*, *Cladonia* spp., *Lycopodium complanatum*, and a diversity of lichens and mosses. On the exposed steep slopes of the southern periphery, *Dryas integrifolia*, *Shepherdia canadensis*, juniper, and *Arctous rubra* are abundant.

From the above conspicuously cursory account of the vegetation of the present area of study it is clear that the primary factor which influences the vegetation concerns the nature of the substratum; that is, the directly operative factors are edaphic, being determined by the climate, geology, and topography of the region.

Until observation and analysis of the vegetation have been carried out for many years, there is no basis for a complete study of the succession of communities in this region. The only available accounts of the vegetation, by Shelford and Twomey (61), and McClure (39), both attempt to fit the floristic and ecological facts to an apparently 'a priori' hypothesis of succession and climax. For example, it is implicit from the diagram of McClure ((39), p.18)

that a convergence of vegetation to the climax high tundra – the lichen–heath of Shelford and Twomey (61) – is assumed. Neither account offers any conclusive evidence to support this view. Doubtless there are processes of plant succession in this tundra region, as elsewhere, but the hypothesis that the various component complexes of vegetation are converging to a "*Cladonia–Ericaceae*" climax takes little account of the prevalence of important factors of the substratum, which, unless we invoke a highly protracted and speculative time factor, will maintain the diverse pattern of so-called 'subclimax' types. For example, the continuous subsoil horizon of permafrost in the peat and till will, it is suggested, maintain conditions of impeded drainage and consequently the mosaic of lakes and peat bogs will remain for a very long period of time. And the implied assumption that, eventually, and after an indeterminate but very long period of time this "sedge meadow" will be replaced by "Cladonia–heath" is scarcely meaningful.

As Shelford and Twomey (61) point out, the process of humus-accumulation is one of the dominant factors which influences the development of the vegetation on sand, rock, and gravel. Many of the dominants of the stable dunes and the ridge communities are mycorrhizal, often ericaceous plants – that is, plants which survive and compete successfully in edaphic conditions of exposed humus over sand and rock. But these substrata bear a highly diverse mosaic of communities, owing to the multiplicity of ecological niches in which plants of different ecological amplitudes find compatibility with the environment. And there are stable communities other than 'climax' which occupy considerable areas and are ecologically important. For example, on the rocky ridge the marginal, cliff, ledge, and crevice habitats are dominated by plants whose tolerances confine them to these sites, such as *Cystopteris*, *Shepherdia*, *Ribes oxyacanthoides*, *Juniperus*, and others; a discrete assemblage of plants forming a stable, permanent, but 'non-climax' community.

The elucidation of the ecological problems of this area requires critical autecological studies accompanied by quantitative analyses of plant cover and density. The above account is submitted merely as a preliminary survey to such work.

IV. An Annotated Catalogue of the Native Plants

The following catalogue of plants has been compiled from lists in literature, various herbarium specimens which have been made available, and the collections and observations of the writer. Each species is named and the *more common* synonyms, if any, are appended. As neither the writer's experience of the flora nor his material are adequate to justify taxonomic changes, apart from two minor transfers no innovations are suggested here; however, some attempt has been made to align the nomenclature with recent European floras, particularly that of Clapham, Tutin, and Warburg (15), but always the synonym which is in common use in North America is given. Reference is made to the herbarium exsiccate which was studied and, if available, the number of the sheet is noted. The abbreviations for herbaria which are used are

as follows: H.DAO.—Herbarium of the Botany and Plant Pathology Laboratory, Department of Agriculture, Ottawa; H.NM.—Herbarium of the National Museum of Canada, Ottawa; H.Man.—Herbarium of the University of Manitoba, Winnipeg; H.DRNL.—Herbarium of the Defence Research Northern Laboratory, Fort Churchill, Manitoba; H. Beckett—private herbarium of Mrs. Eva Beckett, Churchill; H.R.—the present author's private herbarium.

Following this the author and year of any publication in which the species was recorded for Churchill are given. Where available, some brief autecological notes are supplied, largely based on the author's field observations. Finally, the general distribution and affinities of the plant are noted, followed by an outline of its area in North America. In this connection it should be noted that 'circumpolar' is used in the loose sense referred to by Hultén ((25), p. 121), that 'boreal' describes an area which coincides approximately with the zone of the Northern Coniferous Forest, that 'arctic' refers to the northern, consistently treeless areas defined by Polunin (44), and that 'subarctic' describes the intermediate, partly forested zone between the true arctic and the continuous forest – the taiga and forest tundra of Hustich (28).

Equisetum arvense L. var. *boreale* (Bong.) Ledeb.

H.R. *550*; Grønntved (21), Gillett (20).

Widespread in the area, seldom locally abundant, it is found on damp calcareous sand and gravel and, less commonly, on organic substrata, particularly on the mossy humus of bogs and lake margins.

Circumpolar, the species cosmopolitan; the variety from Alaska and British Columbia to Northern Labrador and Gaspé; throughout the Canadian Arctic.

Equisetum fluviatile L. (= f. *linnaeanum* (Döll.) Braun.)

H.R. *567*; Gillett (20).

This species is confined to the vegetation of the plain, assuming local abundance in peat bogs in the spruce forest and along the margins of open lakes and tarns.

Circumpolar, boreal; Alaska, British Columbia, and Oregon to Labrador, Newfoundland, and Virginia. At Churchill, near its northern limit for the central plains.

Equisetum variegatum Schleich.

H.R. *468*; Johansen (31), Gillett (20).

Here it is confined to sandy pools and wet flushes, forming a small continuous zone in the peripheral vegetation of pools in sheltered depressions behind the stable dunes of the shore; in such habitats it is commonly associated with *Juncus arcticus*.

Circumpolar, arctic, and subarctic montane; Alaska and California to Ellesmere, Baffin, Newfoundland, and New Jersey.

Lycopodium selago L. *appressum* Desv.

H.DAO. *2235*; Gillett (20).

Also observed just south of our area at Mile 474 (Herb. Beckett, 1954) and at Lamprey (Radforth (49)), the specimen cited was found in a wet rock crevice. It is very rare in the area.

Circumpolar, throughout arctic and boreal regions, montane; Alaska, Colorado (mountains) throughout the Arctic to Labrador and North Carolina.

Lycopodium annotinum L. var. *pungens* (LaPylaie) Desv.

H.R. *570*; Johansen (31), Gillett (20).

Found in typical tree line transitional vegetation, this species is not common in the region. It is found on wet peaty banks under an open spruce canopy, usually concomitant with *Ledum groenlandicum* and *Andromeda polifolia*.

The whole species, circumpolar boreal (subarctic); Alaska, Oregon, and Colorado to South Baffin, Newfoundland, and New Jersey.

Lycopodium complanatum L.

H.R. *635*; Gillett (20).

Within the area the only record by the author was from Twin Lake Hill where it grows in a thick carpet of *Cladonia* and mosses under a discontinuous canopy of *Picea glauca*.

Circumpolar, boreal; Alaska, Washington, and Idaho to Labrador and Maine. Here it is near its northern limit for the plains.

Selaginella selaginoides (L.) Link.

H.DAO. *9874* (Dore, 1949).

This the only known record from the area and only one plant was found, on "mossy ground, 5 miles S. of Churchill".

Circumpolar, subarctic/boreal montane; Alaska and Colorado (mountains) to Labrador, Newfoundland, and New Hampshire.

Botrychium lunaria (L.) Sw.

H. Beckett (1950); Gillett (20).

Not common in the region, it is apparently restricted to dry sheltered crevices and ledges of the outcrop ridges.

Circumpolar, boreal; Alaska and Colorado to Northern Labrador and Vermont.

Cystopteris dickieana Sim.

C. fragilis (L.) Bernh. var. *dickieana* (Sim.) Moore

H.R. *621*.

This species, not previously recorded for Manitoba, has been found in Alaska by Wiggins (68) who draws attention to the possibility that it might be found throughout North America. Hustich and Pettersson (29) record it from coastal stations in Labrador, and Hadač (23) notes its occurrence in Ellesmereland. Its present distribution is little known, but it appears that it occurs more commonly in North America than has been realized; it has been found in Yukon and near The Pas, Manitoba (specimens in the Herbarium of the University of Manitoba, being reported on by Dr. Doris Löve); the present author collected it from Southampton Island, N.W.T., Canada. Its distribution in Greenland (Larsen (34)) would confirm Wiggin's (68) suggestion that it has been overlooked in North America.

The Churchill plants were found in a crevice in the quartzite ridge of Cape Merry, growing with *Ramischia secunda*, *Poa pratensis*, and divers mosses and lichens. It is distinguished from *C. fragilis* primarily on the texture of the spore wall (cf. Wiggins (68)).

Circumpolar, arctic/boreal (probably cosmopolitan); its area in North America has been mapped in Löve and Freedman (37, in press).

C. fragilis (L.) Bernh.

H.R. *532*; Gillett (20).

This plant is found in crevices and ledges in the outcrop ridges, often associated with *Juniperus communis* and *Ribes hudsonianum*. Sporing material from Churchill has shown that both this and the preceding species occur in the area, in identical habitats. It is difficult to ascribe material with no ripe spores to either taxon as the vegetative differences are not conspicuous. For the present all sterile specimens have been considered as *C. fragilis*.

Circumpolar, cosmopolitan (arctic, boreal, and montane); Alaska and Texas to Labrador, Newfoundland, and Georgia.

Gymnocarpium dryopteris (L.) Newm.

Dryopteris disjuncta (Rupr.) Morton, *Thelypteris dryopteris* (L.) Slosson.

H.DAO. *10157* (Coll. Dore, 1949).

Dore's specimen is annotated—"in deep crack in quartzite on exposed tundra; in protected situation with *Cystopteris fragilis*".

Circumpolar, boreal; Alaska and New Mexico to Labrador, Newfoundland, and Virginia.

Picea glauca (Moench.) Voss

H.R. *641*; Tyrrell (66), Johansen (31), Gillett (20).

At Churchill, *P. mariana* is the chief conifer. However, *P. glauca* occurs on drier sites, and in this area it grows on the exposed rocky ridges and on dry gravel ridges.

American, boreal; Alaska and Wyoming to Labrador, Newfoundland, and North Carolina (mountains).

Picea mariana (Mill.) BSP.

H. Beckett; Tyrrell (66).

The black spruce is the dominant tree of the area, forming closed and discontinuous canopies on the organic substratum of the plains and extending on to the outcrop ridges where it forms small stands of stunted individuals, seldom exceeding 4–5 meters. It occurs very rarely on the stable sand of the shore.

American, boreal (subarctic); Alaska and British Columbia to Northern Labrador, Newfoundland, and North Carolina.

Larix laricina (Du Roi) K. Koch

H.R. *574*; Johansen (31), Grøntved (21), Gillett (20).

This species occurs widely but never abundantly, being associated with *Picea mariana* in the peat bogs and lake margins of the plains.

American, boreal (subarctic); Alaska and British Columbia to Labrador, Newfoundland, and New Jersey.

Juniperus communis L. var. *depressa* Pursh.

H.R. *535*; Johansen (31), Grøntved (21), Gillett (20).

It occurs in local abundance on the inland flank of the outcrop ridge of Cape Merry, growing in the ledges and crevices of the low cliffs and boulder screes; it also occurs on the exposed summits of the ridges, in shallow dry humus with *Dryas integrifolia*, *Cetraria nivalis*, *Loiseleuria procumbens*, and *Vaccinium uliginosum*.

The species circumpolar, boreal (subarctic), montane; the variety, from Hudson Bay and Utah to Labrador, Newfoundland, and New York.

Sparganium angustifolium Michx.

H.R. *581*.

This species occurs locally in shallow rocky pools on the ridge, forming the outer zone of submerged aquatic vegetation.

Circumpolar, boreal; Alaska and California to Labrador and Newfoundland.

Sparganium hyperboreum Laestad.

H. Beckett, 1954; Gillett (20).

Found in the marginal vegetation of a pool on the ridge at Cape Merry (Beckett, by personal communication).

American, boreal (subarctic); Alaska and Idaho to Labrador and Newfoundland.

Potamogeton filiformis Pers. var. *borealis* (Raf.) St. John

H.R. *458*; Gillett (20).

Occurring submerged in slow-moving parts of streams (Gillett (20)), and of local occurrence in rock pools over quartzite with *Hippuris vulgaris* and *Juncus arcticus*.

Circumpolar, boreal; Alaska and Colorado to Newfoundland, Quebec, and Maine.

Potamogeton alpinus Balbis ssp. *tenuifolius* (Raf.) Hultén

H.DRNL.; Gillett (20).

Occurring in a small stream in the peat bog plain (Gillett (20)).

American, boreal; Alaska and Colorado to Labrador, Newfoundland, and Pennsylvania.

Potamogeton gramineus L.

H.DRNL.; Gillett (20).

This is reported (Gillett (20)) from a drainage ditch near the railway at Churchill.

American, boreal; Alaska and New Mexico to Labrador, Newfoundland, and Pennsylvania.

Triglochin maritima L.

H.R. *454*, *508*, *576*; Johansen (31), Gardner (19), Grøntved (21), Gillett (20).

A species of frequent occurrence in the area, usually in wet peat with sedges; also found in the marshy flats near the Churchill River.

Circumpolar, boreal subarctic; Alaska and California to Labrador, Newfoundland, and New Jersey.

Triglochin palustris L.

H.R. *537*; Gardner (19), Gillett (20).
A plant of local occurrence, it grows in eutrophic peat bogs over gravel.
Circumpolar, boreal; Alaska and New Mexico to Labrador, Newfoundland, and New York.

Festuca brachyphylla Schultes

H.R. *645*; Johansen (31), Gillett (20).
It occurs in considerable quantity on the gravel/sand foreshore area of the beaches, usually accompanied by ***Elymus mollis***.
Circumpolar, arctic montane; Alaska and California (mountains) throughout the Arctic to Labrador, Newfoundland, and New England.

Puccinellia lucida Fern. and Weath.

H.DRNL.; Gillett (20).
Recorded from the wet foreshore sand near Fort Churchill.
American, boreal; British Columbia and California to Hudson Bay and Gaspé.

Puccinellia langeana Th. Sør.

P. paupercula (Holm.) Fern. and Weath., *Glyceria langeana* Beul.
H.DAO. *2570*, *2571*; Gillett (20).
The specimens cited were collected from "fine wet gravel on the beach at tide level" – in the vicinity of Fort Churchill. Sørensen (62, p. 21) points out that this is the subarctic species of Eastern Canada which has been identified with *P. paupercula*.
American (and Greenland), subarctic; north coast of Alaska, coastal Hudson Bay, Labrador, and Southeastern Quebec.

Puccinellia phryganodes (Trin.) Scribn. and Merrill

H.DAO. *2539*; Gillett (20).
This is rare in our area; the specimens cited were collected from the sandy gravel of the foreshore near Fort Churchill.
Circumpolar, arctic maritime; from Alaska to Labrador, confined to the coasts and throughout the Arctic.

Poa pratensis L.

H.R. *460*; Gillett (20).
Common throughout the area, varying considerably, this species was found, apparently as a native plant, in dry humus over rock on the outcrop ridges. Much of the material constitutes introductions from southern parts.
Circumpolar, arctic (boreal); Alaska and Mexico to Northern Labrador; throughout the Canadian Arctic.

Poa arctica R. Br.

H.R. *523*; Johansen (31), Gillett (20).
A common component of the heath vegetation of gravel and rock ridges, it often forms local swards in shallow humous soil.
Circumpolar, arctic montane; Alaska and British Columbia throughout the Arctic to Labrador, Newfoundland, and Eastern Quebec.

Poa alpina L.

H.R. *431*; Gillett (20).
The author's material is referable to var. *bivonae* (Parl.) St. John. It appears to be fairly common on exposed gravel and rocky ridges, growing in shallow, dry humous soil.
The species circumpolar, arctic montane; Alaska and Colorado to Labrador, Newfoundland, and Nova Scotia.

Poa glauca Vahl.

H.R. *543*; Johansen (31), Gillett (20).
This common grass is found on dry sites on calcareous gravel ridges, often forming a conspicuous part of the vegetation.
Circumpolar, arctic (subarctic) montane; Alaska and British Columbia to Labrador, Newfoundland south to about 43° N.; throughout the Arctic.

Roegneria violacea (Hornem.) Meld.

Agropyron violaceum (Hornem.) Lange.
H.R. *636*.
The only record of this plant is from Twin Lake Hill where it was found on a dry gravel slope with *Shepherdia canadensis* and *Solidago multiradiata*.
American, boreal; Alaska and Mexico to Labrador, Newfoundland, and Maryland.

Elymus mollis Trin.

E. arenarius L. var. *villosus* Mey.
H.R. *432*; Johansen (31), Gardner (19), Grφntved (21), Gillett (20).
This is the dominant plant of the dry sand deposits along the coast, particularly in areas where there has been disturbance. It forms an important part of the community on dry stable sand, frequently concomitant with *Castilleja raupii* and *Arctous rubra*. Rarely, it extends into the scrub spruce wood on the ridge where it is confined to dry, open ledges.
American–Asian, arctic coastal; Alaska and California, throughout the Arctic to Labrador, Newfoundland, and Massachusetts.

Elymus innovatus Beal.

E. mollis R. Br.
H.DAO. *2539*; Gillett (20).
The specimen cited above was collected on a "gravel railroad embankment, Warkworth Creek".
American, boreal montane; Alaska and California to Hudson Bay and Massachusetts; here near its northern limit for the plains.

Trisetum spicatum (L.) Richter (including var. *molle* (Michx.) Beal.)

H.R. *542*, *603*; Gardner (19), Gillett (20).
This grass is common in the area, observed by the author as a consistent component of the vegetation on gravel ridges and coastal sand and gravel flats.
The species, circumpolar, arctic montane; Alaska and British Columbia throughout the Arctic to Labrador, Newfoundland, and Maine.

Deschampsia caespitosa (L.) Beauv. var. *littoralis* (Reut.) Richter

H.DAO. *2368*; Gillett (20).
Gillett's specimen was collected on the gravel bank of a stream.
Circumpolar, arctic; Alaska and Colorado to Labrador, Newfoundland, and Gaspé; common in the southern Arctic.

Arctagrostis latifolia (R. Br.) Griseb.

H.R. *522*; Johansen (31), Grφntved (21), Gillett (20).
Common throughout the area, it is found on damp humous substrata over both gravel and rock; apparently more common in eutrophic conditions.
Circumpolar, arctic; Alaska and British Columbia to Northern Labrador; throughout the Canadian Arctic.

Calamagrostis canadensis (Michx.) Nutt.

Most of the Churchill material seems to be referable to var. *scabra* (Presl.) Hitchc.
H.R. *648*; Grφntved (21), Gillett (20).
Apparently never common, it occurs in damp humous sites on the sheltered flanks of the rocky ridges.
American, boreal; Alaska and California to Labrador, Newfoundland, and Maryland.

Calamagrostis inexpansa A. Gray

H.DRNL.; Gillett (20).
This species is found on exposed gravel ridges, often in open communities on the summits.
American, boreal; Alaska and New Mexico to Newfoundland and Maine.

Calamagrostis deschampsoides Trin.

H.NM. (Porsild, 1930, *5378*); Gillett (20).
Incompletely circumpolar, subarctic montane; Alaska and California to west coast of Hudson Bay. Here at its eastern limit in North America.

Calamagrostis neglecta (Ehrh.) G.M. and S.

H.DAO.; Gillett (20).

Gillett's specimen was found on gravel near the airfield at Fort Churchill.

Circumpolar, arctic; Alaska and Colorado to Labrador and Maine, common in Arctic of Canada.

Hierochloe odorata (L.) Beauv.

H.R. *540*; Gillett (20).

A common plant on the open sandy gravel of the foreshore community and on the summits of limestone gravel ridges.

Circumpolar, boreal (in North America); Alaska and Nebraska to Northern Labrador, Newfoundland, and New Jersey.

Beckmannia syzigachne (Steud.) Fern.

H.DAO. *2381*; Gillett (20).

The present author did not record this species; Gillett's exsiccate is annotated – "in gravel area, rare. Fort Churchill".

American, boreal; Alaska and New Mexico to Quebec and Ohio.

Eleocharis fernaldii (Svenson) Löve

E. pauciflora (Lightf.) var. *Fernaldii* Svenson

H.DRNL.; Gillett (20).

Locally common in wet situations on the river flats and in rock pools on the gravel deposits, it is not widespread in the area.

American, boreal; Yukon and Iowa to Newfoundland and Gaspé, south to New York.

Eleocharis palustris (L.) R. & S.

H.R. *481*; Gillett (20).

Forming small local pure stands, it occurs in depressions on the rocky ridge, often in dried-out pools, with its rhizomes in wet, decomposing peat.

(Until this group has been studied more thoroughly, no attempt will be made to distinguish *E. smallii* Britton which has been recorded from this area by Gillett (20)).

Circumpolar, boreal; Alaska and Oregon to Labrador, Newfoundland, and New England.

Trichophorum alpinum (L.) Pers.

Scirpus hudsonianus (Michx.) Fern.

H.R. *554*; Gillett (20).

This plant is not common over the area, but it forms local facies in suitable habitats; it grows in wet shallow peat, often over calcareous gravel; common concomitants are *Oxycoccus microcarpus* and *Rubus chamaemorus*.

Circumpolar, boreal; Alaska and Montana to Labrador, Newfoundland, and Connecticut.

Trichophorum caespitosum (L.) Hartm.

Scirpus caespitosus L. var. *callosus* Bigel.

H.R. *444*; Gillett (20).

Occurring sporadically over the area, it grows in small tussocks in wet, humous soil over gravel at the edge of ponds on the rocky ridge.

Circumpolar, subarctic montane; Alaska and Colorado, in the Southern Canadian Arctic, to Northern Labrador, Newfoundland, and New York.

Eriophorum brachyantherum Trautv. & Mey.

E. opacum (Björnstr.) Fern.

H.R. *470*.

The only record, found in local abundance in a small peat bog at the margin of a pool on the outcrop ridge east of Cape Merry.

Circumpolar, subarctic montane; Alaska and Southern British Columbia to Southeast Labrador and Southern Ontario.

Eriophorum spissum Fern.

E. callitrix Fern.

H.DAO. *1880, 1924* (Gillett); Gillett (20).

Not common here, it was recorded (Gillett) on the "edges of hummocks in sedge meadow".

American, arctic montane; Alaska and Alberta to Northern Labrador, Newfoundland, and New York; in the Canadian Arctic to about 65°N.

Eriophorum callitrix Cham.

H.Man. (Beckett, *168*).
American (Eastern Asia), subarctic montane; Alaska and Montana (mountains) to Labrador and Newfoundland.

Eriophorum callitrix Cham. var. *moravium* Raymond

H.DAO. *100025* (Dore).
Dore's specimen from Churchill was found in a "wet peaty meadow on rocky tundra near shore".
Apparently subarctic, known from Great Bear Lake (N.W.T.), Churchill, and Labrador (Raymond, 1956).

Eriophorum russeolum Fries. var. *albidum* Nylander

E. Chamissonis var. *albidum* Fern.; *E. russeolum* var. *leucothrix* Hult.
H.DAO. *1973*, *1925* (Gillett); Gillett (20).
Circumpolar (incompletely), arctic montane; Alaska to North Baffin, Gaspé, and James Bay.

Eriophorum chamissonis C. A. Meyer

H.R. *477a*.
Only one small collection of this plant was made, from the margin of a small peaty pool on the ridge at Cape Merry.
American (Eastern Asia), boreal montane; Alaska and Oregon to Hudson Bay and Newfoundland.

Eriophorum scheuchzeri Hoppe

H.R. *470*.
Locally common, this species is found in the marginal vegetation of peaty pools, both on the rocky ridges and in the plain.
Circumpolar, arctic; Alaska and British Columbia to Northern Quebec and Newfoundland; throughout the Arctic; here it is near its southern limit.

Eriophorum angustifolium Roth.

H.R. *456*; Johansen (31), Gardner (19), Gillett (20).
Common in wet peat at the margins of shallow pools, it forms pure stands of local occurrence.
Circumpolar, arctic–subarctic; Alaska and Oregon to Northern Labrador, Newfoundland, and New York; throughout the Canadian Arctic.

Carex capitata L.

H.R. *449*.
This sedge is common in the damp mossy humus of the spruce woods on the rocky ridge, usually concomitant with *Orchis rotundifolia*, *Tofieldia pusilla*, and *Carex concinna*.
Circumpolar, subarctic montane; Alaska and Labrador, Southeastern Arctic, montane in Quebec, New Hampshire, and Western America.

Carex diandra Schrank.

H.DRNL.; Gillett (20).
Infrequent here, it has been recorded from the semiaquatic habitats of pool margins on the ridge and plain, growing in wet peat.
Circumpolar, boreal; Alaska and Colorado to Labrador and Pennsylvania.

Carex amblyorhyncha Krecz.

H.NM. (Duman, *1296*, 1938).
This material, originally determined as *C. neurochlaena* Holm. by Duman (16, 17), has been described and discussed by Böcher (10). It occurs, sporadically, in wet peat bogs.
Incompletely circumpolar, arctic; in America it is apparently disjunct, though it is a seldom collected species and might be more common than is known; it occurs in Alaska and Yukon and in the region of Northern Hudson Bay, with an isolated occurrence in James Bay (after Böcher (10, p. 27)).

Carex marina Dewey

C. bipartita Bellardi var. *amphigena* (Fern.) Polunin
H.Man. (E. Beckett, 1953).
Occurring locally, this specimen was found in an open peaty area on the Cape Merry ridge east of the Churchill township.
Circumpolar, arctic (coastal); Alaska and British Columbia to Labrador, Gaspé, and New Brunswick; throughout the Canadian Arctic.

Carex gynocrates Wormskj.

H.R. *557*; Gillett (20).
This species was collected from near Fort Churchill and observed at many other localities in the area. It grows in damp peaty soils over base-rich till, often concomitant with *Carex vaginata* and *Trichophorum alpinum*.
American, subarctic–boreal, montane in the south; Alaska and Colorado to Newfoundland and New York.

Carex mackenziei Krecz.

C. norvegica Willd.
H. Beckett (Coll. 1950).
Polunin (42) notes that this species was "fairly plentiful along the river estuary . . .".
American (Greenland), subarctic maritime; Alaska to Southeast Quebec.

Carex scirpoidea Michx.

H.R. *420*; Grøntved (21), Gillett (20).
One of the commonest sedges in the area, it is found abundantly on damp humous substrata, in open spruce scrub on the outcrop ridges, and in peat bogs and along the flanks of the rocky ridges.
Circumpolar, arctic montane; Alaska and Washington (mountains) to Labrador and Maine; throughout the Eastern Arctic except the far North.

Carex concinna R. Br.

H.R. *445*; Gillett (20).
Not a common sedge in the area, it was collected in the spruce scrub vegetation of the outcrop ridge east of Cape Merry, where it was growing in a mossy, humous substratum.
American, boreal (subarctic); Alaska and Colorado (mountains) to Newfoundland and Gaspé.

Carex glacialis Mack.

H.R. *527*; Gillett (20).
A local species, forming tussocks on the dry gravelly sand of the foreshore dunes contiguous with the outcrop ridge; often concomitant with *Arctous rubra* and *Castilleja raupii* on stable sand.
Circumpolar, arctic montane; Yukon to Newfoundland, in the Arctic; here near its southern limit for the Hudson Bay region.

Carex bicolor Bellardi ex All.

H.NM. *21691* (Coll. A.E. Porsild, 1930); Johansen (31).
(No ecological information)
Circumpolar, subarctic montane; Alaska, through low-Arctic Canada to Hudson Bay and Newfoundland.

Carex aurea Nutt.

H. Beckett (1954).
On an open, peaty area on the ridge between Fort Churchill and the township; apparently the only record from the area.
American, boreal; Alaska and New Mexico to Southern Labrador, Newfoundland, and Connecticut.

Carex vaginata Tausch.

H.R. *438*, *459*; Gillett (20).
Confined to bog vegetation, this plant occurs throughout the area. It is commonly associated with bog species characteristic of eutrophic conditions, such as *Carex rariflora*, *Primula egaliksensis*, *Pedicularis flammea*, and others.
Circumpolar, low-arctic/boreal; Alaska and British Columbia to Labrador and New York.

Carex capillaris L. (c.f. Boivin(11))

H.DAO. *2229*, *2430*; Gillett (20).
Gillett records it from the community on a dried up pool over sand.
Circumpolar arctic montane (boreal); Alaska and New Mexico (mountains) throughout the south of the Eastern Arctic, to Labrador, Newfoundland, and New Hampshire (mountains).

Carex capillaris L. var. *porsildiana* Polunin

H.DAO. *1352* (Coll. Duman, 1938).
Arctic, from Alaska to Labrador and Iceland; here near its southern limit.

Carex williamsii Britton

H.NM. *22606* (Polunin, 1936), Raymond (54).
American, subarctic; Alaska, Yukon, Keewatin, and Quebec (Ungava).

Carex atrofusca Schkuhr.

H.R. *518*; Gardner (19), Gillett (20).
Not common in the area, the present author recorded it only at Christmas Lake where it grew in a eutrophic bog flanking a gravel ridge, in a rich sedge meadow with *Pedicularis flammea*, *Coptidium lapponicum*, and *Epilobium palustre*.
Circumpolar, arctic montane; Alaska, throughout the Canadian Arctic to Northern Labrador; here at its southern limit in the plains.

Carex rariflora (Wahl.) Sm.

H.R. *519*, *551*; Johansen (31), Gardner (19).
Common throughout the area, this species is found on wet, deep peat bogs, often assuming local abundance; in some areas there is evidence that it tolerates locally base-rich conditions.
Circumpolar, subarctic montane; Alaska to Baffin, Labrador and Newfoundland, south to Maine (mountains).

Carex limosa L.

H.R. *551*; Gillett (20).
This sedge is locally common in the wetter areas of peat bogs and in the submarginal vegetation of ponds.
Circumpolar, boreal alpine; Alaska and Colorado (mountains) to Labrador, Newfoundland, and south to 40°N.

Carex norvegica Retz.

C. Halleri Gunn.
H.DAO.
Collected by Dore he notes that it grew on a "S. facing slope of runway embankment, forming dense clones Fort Churchill".
Circumpolar, low-arctic montane; Keewatin and Manitoba to Baffin, Labrador, and Gaspé.

Carex media R. Br.

C. norvegica Retz. ssp. *inferalpinum* (Wahl.) Hult.
H.Man. (E. Beckett, 1953).
This specimen was collected east of Churchill township on a peaty area on the ridge of Cape Merry.
Circumpolar, boreal; Alaska and Idaho to Labrador, Newfoundland, and New Brunswick.

Carex adelostoma Krecz.

C. polygama Schultz. ssp. *alpina* (Hartm.) Cajander.
H.R. *558*.
This species grows near Farnworth Lake in a wet, open peat bog with sparse spruce cover; its concomitants are *C. vaginata*, *C. gynocrates*, and *Platanthera hyperborea*.
This appears to be only the second record of this species for North America, the other locality being in Northern Labrador (Raymond (54, 57)).
This considerable extension of the known area of the species is the more remarkable since it is one of the amphi-Atlantic species of Arctic affinities (Raymond (57)). Raymond (54) and (56) has indicated the North American and world distribution on maps. However, it is difficult to make a clear distinction between some specimens of *C. Morrisseyi* Porsild and this material, and further study of the group in North America is desirable.

Carex aquatilis Wahl.

H.R. *521*; Johansen (31), Gillett (20).

Common throughout the area, this sedge forms narrow zones at the margins of lakes and streams.

Circumpolar, arctic montane; Alaska and New Mexico (mountains), throughout the Eastern Arctic, to Labrador, Newfoundland, and New York.

Carex microglochin Wahl.

H.R. *501*; Grφntved (21), Gillett (20).

This plant is found in damp, peaty flushes on the coastal sand of Cape Merry; its occurrence with *Primula stricta*, *P. egaliksensis*, and *Parnassia multiseta* indicates that it is a plant of base-rich soil preferences.

Circumpolar, subarctic montane; Alaska and Colorado (mountains) to Labrador, Newfoundland, and Southern Quebec.

Carex maritima Greene

C. incurva Lightf.

H.R. *465*; Johansen (31), Gardner (19), Gillett (20).

A common shore plant at Churchill, occurring both on wet, calcareous sand and gravel flats of the foreshore and on the drier, stable sand adjacent to the rocky ridge.

Circumpolar, arctic montane; Alaska to Northern Quebec and Newfoundland; throughout the Canadian Arctic except the far North.

Carex oligosperma Michx. var. ***churchilliana*** Raymond, n. var.

Planta 15–30 cm. alta, gracillima; foliis angustissimis; spica foeminea singula, 2–3–4-floribus composita. MANITOBA: Churchill. *Eva Beckett*. TYPE in the Herbarium, University of Manitoba.

Differing markedly from the tall (up to 1 meter) and coarse plant of boreal and temperate bogs, this slender and small extreme merits recognition.

Carex miliaris Michx. var. *major* Bailey

C. rhomalea (Fern.) Mackenzie, *C. saxatilis* L. var. *rhomalea* Fern.

H.R. *421*; Gardner (19), Gillett (20).

Common in the area, this plant forms a distinct zone at the margin of pools where it grows in wet, acid peat.

American, subarctic montane; British Columbia to Labrador, Newfoundland, and Maine; in the Southern Canadian Arctic.

Carex membranacea Hook.

H.R. *644*; Grφntved (21).

Uncommon here, it was noted only once by the present author in damp peat on the Cape Merry ridge near the township, growing with *Tofieldia pusilla* and *Arctagrostis latifolia*.

American, arctic; Alaska and Yukon, throughout the Southern Arctic to Baffin and Northern Labrador; near its southern limit in the Hudson Bay region.

Cartex rotundata Wahl.

H.R. *578*; Johansen (31).

Not common, it was found in local abundance at the margin of Farnworth Lake, growing with *Betula glandulosa*, *Comarum palustre*, and *Equisetum fluviatile*.

Circumpolar, arctic montane; Alaska and Mackenzie to Northern Labrador.

Lemna trisulca L.

H.DAO.; Gillett (20).

The only record from the area, found at Warkworth Creek.

Cosmopolitan, boreal, temperate; British Columbia and California to Nova Scotia and Florida.

Juncus arcticus Willd.

H.R. *459*; Gardner (19), Gillett (20).

Not common in the area this plant appears to be confined to wet, sheltered, sandy areas; it forms a narrow marginal zone round sand pools on the seaward flank of the rocky ridge, associated with *Equisetum variegatum* and, in adjacent open water, *Potamogeton filiformis* and *Hippuris vulgaris*.

Circumpolar arctic montane; the whole species from Alaska and California (mountains) to Eastern Labrador and Quebec.

Juncus balticus Willd. var. *littoralis* Engelm.

H.R. *453*; Johansen (31), Gardner (19), Gillett (20).

In the region it appears to be confined to brackish mud flats at the river estuary, and to wet, eutrophic sand in hollows on the margin of the rocky ridge.

Circumpolar (the whole species); the variety American, boreal; Alaska and California to Labrador, Newfoundland, and New York.

Juncus albescens (Lange.) Fern.

H.R. *486*; Johansen (31), Gardner (19), Gillett (20).

Not a common plant in the area, it occurs on wet, humous soil on the rocky ridge, associated with *Tofieldia pusilla* and *Vaccinium uliginosum*.

American, arctic montane; Alaska and Colorado (mountains) to Labrador, Newfoundland, and New York. Here it is near its southern limit in the central plains.

Juncus nodulosus Wahl.

J. alpinus Vill. var. *rariflorus* (Fries.) Hartm.

This plant is seldom found in abundance, being confined to base-rich often calcareous peats over gravel.

Circumpolar, boreal (the whole species); Alaska and Idaho to Quebec and Pennsylvania.

Juncus castaneus Sm.

H.R. *419*; Gardner (19).

Common in the area, it is a constant member of the rich, wet meadow communities, in both the plains and on the rocky ridges; it also forms dense tussocks in wet, calcareous gravel with *Trichophorum caespitosum* and *Astragalus eucosmus*.

Circumpolar, arctic montane; Alaska and New Mexico (mountains) to Labrador and Gaspé; common in the Eastern Arctic; near its southern limit for the plains.

Luzula parviflora (Ehrh.) Desv.

H.DAO. *2604*; Gillett (20).

Gillett's collection is annotated—"common on lake shore under 10′ willows; 4 ml. S.E. of Ft. Churchill".

Circumpolar, boreal; Alaska and Arizona (mountains) to Labrador, Newfoundland, and Massachusetts.

Luzula frigida (Buch.) Sam. var. *contracta* Sam.

L. sudetica (Willd.) DC var. *frigida* (Buch.) Fern.

H. Beckett; Johansen (31).

A common species on the dry, humous substrata of the rocky ridge of Cape Merry.

The whole species, circumpolar, boreal; Alaska and to Labrador, Newfoundland, and Gaspé.

Luzula confusa Lindeb.

L. hyperborea R.Br., *L. arcuata* Wahl. var. *confusa* (Lindeb.) Kjellm.

H.R. *647*; Gardner (19).

This species appears to be confined to exposed, humus-filled crevices on the quartzite ridge, associated with the lichens and prostrate shrubs of the tundra-heath vegetation.

Circumpolar, arctic montane; Alaska and Alberta, throughout the Canadian Arctic to Northern Labrador, Newfoundland, and New Hampshire.

Tofieldia pusilla (Michx.) Pers.

T. palustris auct., *T. borealis* Wahl.

H.R. *411*; Tyrrell (66), Johansen (31), Grønntved (21), Gardner (19), Gillett (20).

Frequent in many localities, this species is most abundant on damp humus on open, rocky tundra, in open sites in the spruce stands on the rocky ridge, and, less commonly, in damp hollows in the sand areas. In all areas the plant is rooted in humous substrata over divers parent materials.

Circumpolar, arctic montane; Alaska and British Columbia to Labrador, Newfoundland, and Gaspé; common in the southern arctic of Canada.

Smilacina trifolia (L.) Desf.

H.R. *552*; Gillett (20).

This plant is confined to wooded areas, occurring both on the ridge and in the plain; in both habitats it grows in wet peat, often at the margin of shallow tarns.

Circumpolar, boreal montane; British Columbia to Labrador, Newfoundland, and New Jersey.

Cypripedium passerinum Richards.

H.R. *455*; Grønntved (21), Gillett (20).

Here it is confined to clearings and crevices in the spruce wood on the quartzite ridge where it forms occasional clumps on damp humous soil, associated with *Bartsia alpina* and *Geocaulon lividum*.

American, boreal; Alaska and Alberta to Southern Quebec (Mingan Is.).

Orchis rotundifolia Pursh.

H.R. *410*; Tyrrell (66), Johansen (31), Grønntved (21).

Like the preceding, it is confined to the drier ridge communities, being locally abundant on the dry, humous, mossy substratum of spruce woods, closely associated with *Platanthera obtusata*.

American, boreal; Alaska and Southern British Columbia to Newfoundland, Southern Quebec, and New York.

Platanthera hyperborea (L.) Lindl.

Habenaria hyperborea L.

H.R. *612*; Grønntved (21), Gillett (20).

A common species of eutrophic, wet peat, it has been noted in peat bogs of the spruce/barren-land transition, and in the flushed sandy hollows near the sea with *Tofieldia*, *Primula stricta*, and *Epilobium palustre*.

American, (Iceland and Greenland) boreal; Alaska and Colorado to Ungava, Labrador, and New York. Near its northern limit here for the plains.

Platanthera obtusata (Pursh.) Lindl.

Habenaria obtusata (Pursh.) Richards.

H.R. *417*; Gardner (19), Gillett (20).

Not common, it grows in damp habitats of the spruce woods on the outcrop ridge, usually associated with *Orchis rotundifolia* and *Tofieldia pusilla*.

American, boreal; Alaska and California to Labrador, Gaspé, and New York.

Spiranthes romanzoffiana Cham.

H.R. *562*; Gillett (20).

Not common in the area, this species is confined to the region of bogs and sedge meadows; it was recorded by the author in a peat bog along with *Carex vaginata*, *Platanthera hyperborea*, and *Rubus chamaemorus*.

American (amphi-Atlantic), boreal; Alaska and Colorado to Labrador, Newfoundland, and New York.

Listera borealis Morong

H. Beckett (Coll. 1950).

Mrs. Beckett recorded this species on the west side of the Churchill River where it grew sporadically in shaded, humous habitats under spruce.

American, boreal montane; Alaska and Colorado (mountains) to Newfoundland and South-east Quebec.

Corallorhiza trifida Chatelain

H.R. *450*, *525*; Gillett (20).

Neither widespread nor locally abundant, it is found in spruce woods on the outcrop ridges growing damp, mossy humus.

Circumpolar, boreal; Alaska and Washington to Labrador and New Jersey.

Salix reticulata L.

H.R. *426*; Güssow (22), Johansen (31), Gillett (20).

Throughout the region it is most common on dry, heathy sites; on the outcrop ridges and the stable dune communities it is locally dominant. It occurs occasionally in the spruce scrub of the ridges and on certain gravel ridges. One specimen has been separated as var. *subrotunda* Seringe. It was collected on the rocky terrain of the scrub spruce wood near Fort Churchill (H. R. 426*a*).

Circumpolar, arctic montane; Alaska and Northern British Columbia to Southeastern Labrador and James Bay; throughout the Canadian Arctic to 75°N.

Salix vestita Pursh. var. *erecta* Anderss.

H.NM. (Coll. J. M. Macoun, *79143*); Gillett (20).

The whole species, American subarctic; British Columbia and Oregon to Northern Labrador and Southeastern Quebec; the variety western; here at its northern limit in the Hudson Bay region.

Salix anglorum Cham.

S. arctica Pall. var. *Brownei* Anderss. (in part?).

H. C. R. Ball, Coll. N. B. Sanson (1938). cf. Ball (2).

Ball (2) gives the distribution of this species as Alaska, British Columbia, and Montana to Northern Baffin and Labrador.

Salix arctophila Cockerell

H.R. *409*; Gillett (20).

A common willow in the area, it grows in damp, humous soils, on the outcrop ridges in sheltered crevices, on the stable dune community, and, less commonly, in peat bogs of the plain.

American, arctic montane; Alaska, throughout the low-Arctic to Northern Labrador, Newfoundland, and Maine (mountains); an eastern species.

Salix glauca L. var. *acutifolia* (Hook.) Schneider

H. Beckett (1954); Johansen (31), Gardner (19).

Apparently not common in the region, it has been recorded from the sheltered flanks of the outcrop ridge on the east side of the river.

The whole species, circumpolar, subarctic montane; Alaska and Southern British Columbia, throughout the southern Arctic to Southern Baffin, Northern Quebec, and James Bay; a western species.

Salix desertorum Richards.

H.R. *436*, *505*, *530*; Gillett (20).

This plant grows in a wide range of habitats; the present author recorded it on limestone ridges, from the fringe of the scrub spruce of the outcrop ridges, and lake-margin communities on the ridges. (The divers problems concerning the taxonomy of this group (Raup (52, 53), Polunin (42) are well known; as the present author has neither the experience nor the material to discuss this and other questions, the treatment of the genus is according to Dr. C. R. Ball who kindly revised the material.)

Apparently, depending on the taxonomic interpretation, an American subarctic species; from Alaska throughout the subarctic to Northern Labrador and the Hudson Bay region (incompletely known).

Salix callicarpaea Trautv.

S. cordifolia Pursh. var. *callicarpaea* (Trautv.) Fern.

Gillett's collection is annotated – "common on gravel area, Fort Churchill". Because of the difficulty of distinguishing the varieties of this species in the field, little information can be provided here about their habitats.

American, arctic montane; from Somerset Island and Western Hudson Bay to Northern Labrador and Gaspé.

Salix cordifolia Pursh. var. *tonsa* Fern.

H.R. *506* (apparently new to Manitoba).

Distinguished by the large leaves and completely glabrous leaves and twigs (Dr. Ball, private communication), this variety appears to be common along the sandy shores in the area, extending on to the flanks of the rocky ridges from the stable sand heaths.

American, subarctic montane; Churchill, Northern Labrador and Southeastern Quebec.

Salix brachycarpa Nutt. var. *antimima* (Schneider) Raup.

H.Man. (E. Beckett 1950); Gardner (19), Gillett (20).

Apparently widespread, though never common, it is a species of damp humous substrata, occurring on the rocky ridge and the sand heaths.

American, subarctic montane; from Northwest Mackenzie, Husdon Bay, and Gaspé (discontinuous area).

Salix brachycarpa Nutt. var. *mexiae* Ball

H.R. *618*; (Apparently a new record for Manitoba).

The specimen was collected in a dune 'slack' area near Fort Churchill, growing in wet, eutrophic soil conditions.

American, montane boreal; a western variety, here at its eastern limit.

Salix myrtillifolia Anderss.

H.R. *531*; Gillett (20); also possibly Grønvted (21) as suggested by Raup ((52), p. 111).

This shrub is common in shallow bogs and marshes over calcareous gravel, often occurring along the lower flanks of gravel ridges; it also grows on stream and lake margins.

American, boreal montane; Alaska and Southern Alberta to Newfoundland and Gaspé; here at its northern limit; a western species.

Salix adenophylla Hook.

Grønvted (21), in Raup (52).

No ecological information is available and the specimen (Birket-Smith 1065*a*) has not been examined.

American, boreal; Churchill and Northern Michigan to Southern Labrador, Gaspé, and Maine; an eastern species, here at its northern limit.

Salix calcicola Fern. and Wieg.

H.R. *472*; Gardner (19), Gillett (20).

A prostrate shrub, it occurs in damp humous soil over calcareous gravel; it is found in areas on the outcrop ridges and occasionally on the sides of low gravel ridges.

American, low-arctic montane; Northwestern Hudson Bay and James Bay to Baffin, Northern Labrador, Newfoundland, and Gaspé. Eastern.

Salix alaxensis (Anderss.) Cov.

H.R. *504*; Gardner (19), Gillett (20).

This plant is found in sheltered hollows in the rocky ridge and on the stable vegetation of the coastal sands.

var. *obovalifolia* Ball.

H.Man. (E. Beckett, 1953).

Apparently in similar habitats, Raup (52) notes that this variety is common in the Hudson Bay region.

The whole species, American, subarctic montane; Alaska and British Columbia to Hudson Bay; western, here near its eastern limit.

Salix candida Flugge.

H.DAO. *2104* (Gillett, 1948); Johansen (31), Gillett (20).

Recorded by Gillett (20) as a common shrub on the sandy flats of the coastal dunes.

American, boreal; Alaska to Labrador, Newfoundland, and New Jersey.

Salix bebbiana Sarg.

H.Man. (Coll. V. W. Jackson, 1930).

American, boreal; Alaska and New Mexico to Southern Labrador and New Jersey; here at its northern limit for the plains.

Salix pedicellaris Pursh. var. *hypoglauca* Fern.

H.NM. (Gardner, *65*).

American, boreal; British Columbia and Washington to Quebec and New York.

Salix planifolia Pursh.

H.DAO. *1698*; Gillett (20).
This shrub was collected by Gillett and Cody in "*Salix–Carex* flats near Churchill River", at Fort Churchill.
American, boreal; British Columbia and Washington to Labrador, Gaspé, and New Hampshire.

Salix pellita Anderss.

H.R. *534*.
Apparently not common in the area, it was collected from the marginal ridge of a lake on the open tundra of the rocky ridge east of Cape Merry.
American, boreal; Saskatchewan and Michigan to Labrador, Newfoundland, and Vermont.

Salix arbusculoides Anderss.

H.R. *539*; Grøntved (21).
This shrub is not uncommon on dry, well-vegetated limestone ridges.
American, boreal montane; Alaska and British Columbia to Western Hudson Bay; this is the eastern limit.

Myrica gale L.

H.R. *563*; Gillett (20).
Common, though never locally abundant, on the peat bogs with sparse spruce cover, it is usually associated with *Salix* spp. and *Ledum groenlandicum*.
Circumpolar, boreal; Alaska and Washington to Labrador, Newfoundland, and New York.

Betula glandulosa Michx.

H.R. *473*.
A variable species here, it occupies a wide ecological range. It is a frequent dominant of the marginal fringe of shallow tarns, growing on the peripheral ridge which is formed by the action of winter ice. It also grows in damp, peaty soil over quartzite and reaches a stature of 1.5–2 meters in certain sheltered niches on the seaward side of the rocky ridge at Cape Merry.
Circumpolar, subarctic–boreal montane; Alaska and California to Labrador and New York.

Populus balsamifera L.

P. tacamahacca Mill.
H.R. *649*; Tyrrell (66); Gardner (19), Gillett (20).
This tree is not common in the area, being confined to a few gravel deposits. At Twin Lake Hill it grows in local abundance on the dry gravelly soil of the plateau and slopes.
American, boreal; Alaska and California to Labrador, Newfoundland, and Florida. At Churchill it is at its northern limit for the central plains.

Geocaulon lividum (Richards) Fern.

H.R. *580*.
A local but not uncommon species, it is found in the ground vegetation of spruce patches on the dry rocky ridges; it grows in mossy carpets with its long rhizomes in the lower humous strata.
American, boreal; Alaska and Washington to Labrador, Newfoundland, and New York. Here near its northern limit for the plains.

Urtica gracilis Ait.

H.DRNL.; Gardner (19), Grøntved (21), Gillett (20).
Although not collected by the present author it was observed in several localities, usually growing near streamsides and in the wet, humous soil of willow thickets on the flat plains.
American, boreal; Alaska and New Mexico to Newfoundland and Gaspé.

Rumex occidentalis S. Wats.

H.R. *482*, *620*; Johansen (31), Gardner (19), Grøntved (21), Gillett (20).
Not an uncommon plant of the wet, sandy foreshore areas and saline river flats.
American, boreal; Alaska and California to Labrador, Newfoundland, and Quebec.

Bistorta vivipara (L.) S.F. Gray

Polygonum viviparum L.
H.R. *407*; Johansen (31), Grøntved (21), Gillett (20).
A common plant at Churchill it shows considerable ecological amplitude, occurring on the damp, exposed humous soil of the open tundra ridges, on damp peaty soil over gravel, and, frequently, on damp eutrophic sand along the coastal strip.
Circumpolar, arctic montane; Alaska, Washington, and New Mexico to Northern Labrador and New Hampshire; throughout the Canadian Eastern Arctic.

Atriplex patula L. var. *hastata* (L.) Gray

H.R. *596*; Johansen (31), Gardner (19), Gillett (20).
This species is common along the coast in our area, occurring in wet sand and mud just above hightide level.
Circumpolar, boreal–temperate; British Columbia and California to Newfoundland and South Carolina; here near its northern limit.

Melandrium apetalum (L.) Fenzl.

Lychnis apetala L.
H.Man. (Coll. E. Beckett, No. 76).
Circumpolar, arctic; Alaska to Labrador, throughout the Arctic.

Melandrium gillettii (Boivin) Ritchie, n. comb. based on *Lychnis gillettii* Boivin, in Can. Field-Naturalist, 65 (1), p. 6. 1951.

H.R. *408*; Gillett (1948).
Not common, the author's specimen was found in damp humus of an outcrop on the heathy tundra, with *Dryas* and *Ledum decumbens*.
American, subarctic; known only from Churchill at present.

Stellaria longipes Goldie

H.R. *404*; Tyrrell (66), Johansen (31), Güssow (22), Gardner (20), Grøntved (21).
Common on the heath of the rocky ridge, it grows in damp humus occurring over a wide range of habitats but never in local abundance.
Circumpolar, arctic montane; Alaska and California to Labrador, Newfoundland, and Quebec; throughout the Canadian Arctic.

Stellaria monantha Hultén

H.R. *476*.
This species is common on all humous, damp, and sheltered sites, occurring commonly on the outcrop ridge in protected hollows and crevices.
American/Asian, arctic; Alaska and Washington, throughout the Arctic to Labrador and Gaspé.

Stellaria ciliatosepala Trautv.

H.R. *575*; Gillett (20).
It is common on the flat plain, occurring in marshes and bogs, scattered throughout the vegetation of sedges, mosses, and bog herbs and shrubs.
Circumpolar, arctic; Alaska and Yukon to Northern Baffin and Labrador.

Stellaria calycantha (Ledeb.) Bong.

H.R. *573*; Gillett (20).
A plant of lake and tarn marginal vegetation, it is common throughout the area, occurring in wet peat.
Circumpolar, boreal montane; Alaska and Oregon to Labrador, Newfoundland, and New Jersey.

Stellaria longifolia Muhl.

H.Man. (E. Beckett, 1953).
Locally common in marshy localities on the flanks of the outcrop ridges.
Circumpolar, boreal; Alaska and New Mexico to Labrador, Newfoundland, and Gaspé.

Stellaria crassifolia Ehrh.

H.Man. (E. Beckett, 1953); Gillett (20).
Apparently not very common here, it is found in damp, sheltered parts of the outcrop ridge and adjacent peat areas.
Circumpolar, arctic; Alaska and Colorado to Baffin (south), Newfoundland, and Gaspé.

Stellaria humifusa Rottb.

H.NM. (Polunin, *51715*).
Circumpolar, arctic; Alaska and Oregon to Northern Labrador and Maine; throughout the Canadian Arctic; here near its southern limit for the plains.

Minuartia rubella (Wahl.) Graeb.

Arenaria rubella Wahl.
H.R. *477*; Güssow (22), Gillett (20).
Not uncommon on the rocky ridge, it is found in humus-filled crevices on exposed rocks; occasionally associated with *Saxifraga tricuspidata*.
Circumpolar, arctic montane; Alaska and California (mountains) to Northern Labrador, Newfoundland, and Gaspé; near its southern limit in the central subarctic region; common throughout the Canadian Arctic.

Moehringia lateriflora (L.) Clairv.

Arenaria lateriflora L.
H.DAO. *2148* (Gillett); Gillett (20).
This species is abundant in the area, occurring on gravel, sand and humous substrata; it never forms a dominant facies in the vegetation.
Circumpolar, boreal; Alaska and New Mexico (mountains) to Southern Labrador, Newfoundland, and New Jersey.

Honkenya peploides (L.) Ehrh.

Arenaria peploides L.
H.R. *507*; Johansen (31), Güssow (22), Grøntved (21), Gillett (20).
This sand dune species is common along the shore of the region, being confined to the foreshore, open habitats where it is in the zone of markedly saline conditions. It is found occasionally in disturbed sand hills further from the sea, usually growing with *Elymus mollis*.
Circumpolar, boreal (maritime); Alaska along the arctic coasts to Newfoundland, Quebec, and Maryland.

Cerastium alpinum L.

H.R. *428*; Tyrrell (66), Gardner (19).
Until the taxon is revised (at present being undertaken by Dr. Eric Hultén) the present author ascribes his material to this species *s. lat.* In this area the plant is found chiefly on the coastal ridge and sand dunes where it is scattered on open, dry sites, usually in a stable substratum.
Circumpolar, arctic montane; Alaska and throughout the Rockies, common in the Arctic, to Labrador, Newfoundland, and Southern Quebec.

Caltha palustris L.

H. Beckett (1950).
Mrs. Beckett (private communication) recorded a single patch in marshy ground between Churchill and Fort Churchill, but she has been unable to observe it in subsequent years; this appears to be the only record from the area.
Circumpolar, arctic/boreal; Alaska and Nebraska to Labrador, Newfoundland, and South Carolina; in the Southwestern Canadian Arctic.

Ranunculus sceleratus L.

H.R. *586*; Gardner (19), Gillett (20).
This plant occurs sporadically in shallow pools and springs, often growing with *Batrachium trichophyllum*.
Circumpolar, boreal/temperate; Washington and Oregon to Labrador and Georgia.

Ranunculus purshii Richards.

R. Gmelinii DC.
H.R. *469, 485, 587*; Gillett (20).
This aquatic species is common in shallow pools over calcareous gravel and sand, particularly in the region of the main river estuary.
American, subarctic/boreal; Alaska and Colorado to Southern Labrador, Nova Scotia, and New York.

Ranunculus pedatifidus Sm. var. *leiocarpus* (Trautv.) Fern.

R. affinis R.Br.
H.Man. (E. Beckett 1953).
This plant occurs in ponds on the quartzite ridge of Cape Merry.
Circumpolar, arctic montane; Alaska and Colorado (mountains) to Northern Labrador and Gaspé.

Batrachium trichophyllum (Chaix.) Bosch.

R. trichophyllus Chaix., *R. circinatus* Sibth. var. *subrigidus* (W. B. Drew) Benson.
H.R. *585*; Johansen (31).
A common aquatic found in shallow pools over calcareous gravel in the low flats between the ridges, often associated with *R. purshii* and *Hippuris tetraphylla*.
Circumpolar, boreal; Alaska and Colorado to Labrador and Pennsylvania; here near its northern limit for the plains.

Batrachium subrigidum (W. B. Drew) Ritchie, n. comb., based on *Ranunculus subrigidus* W. B. Drew, Drew (1936), Rhodora 38 p. 39.

Ranunculus amphibius James, *R. subrigidus* W. B. Drew.
H.DAO. *2385, 2489* (Gillett); Gillett (20).
Gillett's specimens were found submerged in a stream and a pool, the latter apparently on the outcrop ridge.
American, boreal; Alberta and Washington to Newfoundland, Quebec, and Massachusetts.

Coptidium lapponicum (L.) Beurl.

Ranunculus lapponicus L.
H.R. *511*; Gillett (20).
The least common *Ranunculus* (*s. lat.*), the specimens cited were collected from a rich peat bog over gravel near Christmas Lake; the plant was concomitant with *Arctagrostis latifolia*, *Carex rariflora*, *Saxifraga hirculus*, and *Primula egaliksensis*.
Circumpolar, subarctic; Alaska and British Columbia to Northern Labrador and Maine; throughout the southern part of the Canadian Arctic.

Cytorhyncha cymbalaria (Pursh.) Britton

Ranunculus cymbalaria Pursh.
H.R. *503, 598*; Grønntved (21), Gillett (20).
Not an uncommon species, though never of ecological importance, it occurs in wet, eutrophic sands, in peat over gravel, and in the foreshore community where drainage is impeded and where it shows halophytic tendencies.
American, boreal/subarctic; Alaska and New Mexico to Labrador and New Jersey; this appears to be the northern limit in the Hudson Bay region.

Anemone multifida Poir. var. *hudsoniana* DC.

H.R. *526*; Johansen (31), Grønntved (21), Gillett (20).
A common sand dune species, found on the fixed and stable dunes with *Elymus*, *Lesquerella*, and *Castilleja raupii*.
American, boreal; Alaska and New Mexico to Newfoundland and New York.

Anemone parviflora Michx.

H.Man. (Beckett 1950); Tyrrell (66), Johansen (31), Gillett (20).
This species grows on Cape Merry, on the rocky ridge being confined to damp, sheltered habitats on the flanks of the ridge.
American, subarctic/boreal; Alaska and Oregon to Northern Labrador and New Brunswick.

Anemone richardsonii Hook.

H.Man. (Beckett 1950); Gillett (20).

Also found on the quartzite ridges, this species grows in damp mossy situations, often at pool margins along the Cape Merry ridge near Churchill township.

American, subarctic; Alaska and British Columbia to Ungava and James Bay.

Draba nivalis Lilj.

H.R. *626*.

Not common in the area, it occurs locally in rock crevices of the outcrop ridge, usually associated with cryptogamic facies.

Circumpolar, arctic montane; Alaska and British Columbia throughout the Canadian Arctic to Labrador and Gaspé; here near its southern limit for the central plains.

Draba minganensis (Vict.) Fern.

H.DAO. *2128*; Gillett (20).

Recorded by Gillett on a dry "burnt over area on the beach flats", Mrs E. Beckett also found it at Sloop's Cove on the west side of the Churchill River, in a sheltered site on the side of the rocky ridge.

American, boreal; from Churchill and James Bay to Southeastern Quebec; here at its western limit.

Draba incana L. (including var. *confusa* (Ehrh.) Lilj.)

H.R. *544*; Tyrrell (66), Gillett (20).

Not widespread in the area, this plant is confined to gravel ridges. It is common on the higher and better drained ridges where it is often concomitant with *Poa glauca*, *Braya humilis*, and various willows.

Circumpolar, (amphi-Atlantic), subarctic; Western Hudson Bay to Newfoundland and Gaspé with southern limit at the Great Lakes; this is the most westerly locality for the plant in North America.

Draba hirta L. emend. O. E. Schultz.

D. glabella Pursh.

H.R. *429*; Gillett (20).

This *Draba* is common in our area, being confined to the rocky ridges. It occurs in damp humous soils in sheltered sites along the ridge flanks.

Circumpolar, subarctic montane; Alaska and British Columbia, throughout the southern part of the Canadian Arctic to Northern Labrador and Quebec.

Draba cinerea Adams

H.Man. (E. Beckett 1950).

Collected by Mrs. Beckett this relatively rare species was found on exposed soil on the outcrop ridge near Churchill.

Circumpolar, arctic; Alaska and Northern British Columbia throughout the Arctic to Ungava and James Bay.

Draba lactea Adams

D. fladnizensis Wulf. var. *heterotricha* (Lind.) Ball.

H.R. *579*.

Not common in the area, this gathering was made in the sparse spruce scrub on the rocky ridge at Fort Churchill; the plants were growing in damp peat over calcareous clay in an open patch.

Circumpolar, arctic; Alaska and British Columbia to Northern Labrador and Eastern Hudson Bay; throughout the Arctic.

Draba alpina L.

H.R. *400*.

Collected earlier by Mrs. Eva Beckett at Churchill, this constitutes an extension southwards of the central North American range of this species. It was found on dry, exposed humus on the rocky ridge of Cape Merry.

Circumpolar, arctic montane; Alaska and British Columbia, throughout the Arctic to Northern Labrador.

Draba nemorosa L. var. *lejocarpa* Lindbl.

H.Man. (Mrs. Beckett, 1950).
Collected on the exposed, humous soil of the Cape Merry ridge.
Circumpolar (the species), boreal; Alaska and Colorado to Hudson Bay and the Great Lakes.

Draba lanceolata Royle

H.DRNL.; Gillett (20).
Circumpolar, boreal (subarctic); Alaska and New Mexico to James Bay, Gaspé, and New Hampshire.

Lesquerella arctica (Wormskj.) S. Watson

H.R. *463*; Gillett (20).
Common on the dry dunes and more or less restricted to this habitat, this species is locally abundant on area of disturbed sand, often associated with *Androsace septentrionalis*.
Circumpolar, arctic; Mackenzie to Labrador and throughout the Canadian Arctic; at Churchill near its southern limit in the plains.

Cochlearia groenlandica L.

C. officinalis L. var. *groenlandica* (L.) Gelert.
H.R. *597*; Gardner (19), Gillett (20).
At Churchill it is confined to open sandy areas of impeded drainage where it is locally frequent, growing with *Atriplex patula* and other halophytes.
Circumpolar, arctic; Alaska to Northern Labrador, throughout the Arctic.

Braya humilis (C. A. Mey.) Robins.

H.R. *545*.
Local at Churchill, this species was observed on calcareous gravel ridges where it was commonly associated with *Draba incana*.
Circumpolar, subarctic montane (absent from Europe); Alaska and British Columbia to Newfoundland and Eastern Quebec.

Rorippa islandica (Oeder) Borbas var. *microcarpa* (Regel.) Fern.

H.R. *566*; Gillett (20).
A common plant in the area, it grows in wet, eutrophic substrata, usually shallow peat over calcareous gravel.
American (the variety), boreal; Alaska and New Mexico to Labrador and Florida.

Barbarea orthoceras Ledeb.

B. vulgaris Cham.
H.Man. (Coll. E. Beckett, 1950).
Common throughout the area, generally in open, disturbed habitats.
American, boreal; Alaska and Colorado to Labrador, Newfoundland, and Maine.

Cardamine pratensis L. *s. lat.*

H.R. *483*; Tyrrell (66), Gillett (20).
Common in the area, it is found in marsh and rich bog vegetation, often over calcareous clay and gravel.
Circumpolar, boreal (subarctic); Alaska and Northern British Columbia to Northern Labrador, Newfoundland, and New Jersey.

Arabis divaricarpa Nels.

H. Beckett (Coll. 1950).
Mrs. Beckett has collected it from a limestone gravel bank south of the township.
American, boreal; Alaska and Colorado to Gaspé and New York.

Arabis arenicola (Richards.) Gelert. var. *pubescens* (Wats.) Gelert.

H.R. *461*; Gillett (20).
In this area it is confined to sandy seashores, being frequently associated with *Lesquerella arctica* in open, dry sand.
American, arctic/subarctic (the whole species); Alaska throughout the southern part of the Eastern Arctic to Northern Labrador.

Saxifraga rivularis L. f. *hyperborea* (R. Br.) Hook.

H.DRNL.; Gillett (20).

Not common here, it was recorded in damp, shaded sites in crevices of the outcrop ridge near Fort Churchill.

The whole species, circumpolar, arctic montane; Alaska and Montana to Labrador and New Hampshire; throughout the Eastern Arctic.

Saxifraga caespitosa L.

S. groenlandica L.

H.Man. (Mrs. Beckett, 1950).

Found on the rocky ridge, in sheltered, shaded crevices, it appears to be of infrequent occurrence here.

Circumpolar, arctic/subarctic; Alaska and Colorado (mountains) to Northern Labrador, Newfoundland, and Gaspé.

Saxifraga tricuspidata Rottb.

H.R. *447*, *400*; Johansen (31), Güssow (22), Gillett (20).

A common saxicolous species, this plant also grows on dry, sandy stable communities. It is found throughout the area, being absent only from bog and forest communities.

American, arctic/subarctic; Alaska and British Columbia throughout the Arctic to Northern Labrador, Newfoundland, and the Great Lakes.

Saxifraga aizoides L.

H.R. *549*, *617*; Grøntved (21), Gillett (20).

This is the commonest saxifrage at Churchill, occurring throughout the area and evincing considerable ecological amplitude. It occurs in the flat, damp, sand dune area with *Primula stricta*, *Parnassia multiseta*, and other plants typical of this eutrophic substratum; it is also found on shallow peat over calcareous gravel; and in the peat bogs of the plain and ridge areas it occurs sporadically, generally associated with locally base-rich conditions of habitat.

Circumpolar, low-arctic montane; Yukon and British Columbia to Northern Labrador and New York; in the southern region of Eastern Arctic. It is one of the wider ranging amphi-Atlantic species.

Saxifraga hirculus L.

H.R. *488*, *512*; Johansen (31), Grøntved (21), Gardner (19), Gillett (20).

A common species of bogs, it occurs in peat communities with evidence of base-rich conditions; usually associated with hypnaceous mosses and such phanerogams as *Primula egaliksensis*, *Coptidium lapponicum*, and *Carex vaginata*.

Circumpolar, arctic/subarctic montane; Alaska and British Columbia, throughout much of the Eastern Arctic, to Labrador; isolated in Colorado and Utah (mountains).

Saxifraga oppositifolia L.

H.R. *475*; Gillett (20).

Occurring in local abundance, this species is an important component of the vegetation of exposed gravel ridge summits; it is uncommon on parts of the dry rocky ridges but completely absent from other habitats.

Circumpolar, arctic montane; Alaska and Idaho to Labrador, Gaspé, and Vermont; abundant and widespread in the Eastern Arctic; at the southern limit for the central plains region.

Chrysosplenium tetrandrum (Lund.) Fries.

H.DAO. *2395*; Gillett (20).

Local in the area, the specimen cited was found in a "sedge meadow by a stream" in the plains region south of Fort Churchill.

Circumpolar, arctic montane; Alaska and British Columbia, throughout the Eastern Arctic to Northern Labrador and the East of Hudson Bay.

Parnassia kotzebuei Cham.

H.R. *451*, *583*; Gillett (20).

This plant is not common at Churchill, being confined to damp, sheltered, humous sites on gravel deposits on the rocky ridge of Cape Merry.

American, subarctic; Alaska and Wyoming to Northern Labrador and Gaspé. At its southern limit in the plains provinces.

Parnassia multiseta (Ledeb.) Fern.

P. palustris L. var. *neogaea* Fern.

H.R. *625*;Tyrrell (66), Johansen (31), Grφntved (21), Gillett (20).

More common than the preceding species, it is found in damp, eutrophic substrata, in clearings in the spruce scrub on the ridges. Also, it is locally common in the flushed dune hollows where it is associated with *Primula stricta*, *Tofieldia*, and other species of eutrophic soil preferences.

Circumpolar, boreal (including the species); the variety, Alaska and Oregon to Labrador, Newfoundland, and the Great Lakes area. Here it is near its northern limit for the plains region.

Ribes hudsonianum Richards.

H.R. *529*; Johansen (31), Gardner (19), Grφntved (21), Gillett (20).

This shrub is found on rocky slopes, in particular on the cliffs and block scree on the landward side of the quartzite ridge, where it grows with such crevice plants as *Cystopteris*, Juniper, and various willows.

American, boreal; Alaska, Oregon, and Utah to Western Quebec and the Great Lakes.

Ribes lacustre (Pers.) Poir.

H.DAO.; Johansen (31), Gardner (19), Gillett (20).

Gillett recorded this near Warkworth Creek where it is a common shrub of the thickets on damp clayey soil.

American, boreal; Alaska and Colorado to Southern Labrador, Newfoundland, and New York.

Ribes triste Pall.

H.Man. (Beckett, 1950); Grφntved (21), Gillett (20).

This prostrate shrub is found under willow scrub in sheltered, lake-side sites on the Cape Merry ridge. (Mrs. E. Beckett).

American, boreal; Alaska and British Columbia to Southern Labrador, Newfoundland, and New York.

Ribes oxyacanthoides L.

H.R. *616*; Grφntved (21), Gillett (20).

In our area this species is not common; the present author recorded it in the damp dune hollows or 'slacks' of the coastal sand where it is associated with *Betula glandulosa* and *Arctous rubra*.

American, boreal/subarctic; Yukon and Montana to Southeastern Hudson Bay and Michigan.

Fragaria glauca (S. Wats.) Rydb.

H.R. *646*; Gillett (20).

Not a common species in the area, it was found as an occasional component of the vegetation of dry gravel banks on the flanks of Twin Lake Hill.

American, boreal; Yukon and Washington to Western Hudson Bay and North Dakota; here at its western limit.

Comarum palustre L.

Potentilla palustris (L.) Scop.

H.R. *569*; Johansen (31), Gillett (20).

This species is confined to peaty pools, where it often assumes dominance; it is usually associated with a variety of sedges and willows.

Boreal (subarctic) circumpolar; Alaska and California to Northern Labrador, Newfoundland, and New Jersey.

Potentilla pensylvanica L.

H.R. *615*, *630*; Johansen (31), Gillett (20).

Sometimes identified with *P. pectinata* Raf. (as by Dr. A. E. Porsild who collected it at Churchill in 1930 – H.NM. *5476*), this plant occurs frequently in the stable community of the upper sand beaches which abut on the rocky ridges; it grows on damp, humous sand.

American, boreal montane; Yukon and New Mexico to Northern Quebec and the Great Lakes; here near its northern limit for the plains.

Potentilla multifida L.

H.R. *493, 629*; Gillett (20).

In this area it appears to be confined to coastal sand deposits, growing in the damp sand of the open *Elymetum* of the fixed dune zone.

Incompletely circumpolar, boreal/subarctic; here it is at its eastern limit in North America.

Potentilla nivea L.

H.R. *439, 490, 494, 628*; Tyrrell (66), Gardner (19), Grøntved (21), Gillett (20).

This elegant perennial is widespread but never locally abundant; it grows in the humous, sandy soil of the stable dunes and is found in humus-filled crevices on the rocky ridges.

Circumpolar, arctic montane; Alaska and British Columbia, throughout the southern Arctic to Labrador, Newfoundland, and Quebec.

Potentilla pulchella R. Br.

H.R. *494, 533, 627, 633, 634.*

Common on the damp sandy soil of the dunes, it occurs in the open community dominated by *Elymus*, locally associated with *Arctous rubra* and *Castilleja raupii*. It was recorded also on the dry summit of a limestone gravel ridge.

Circumpolar (incompletely), subarctic; Alaska, throughout the Canadian Arctic to Baffin Island and Northern Quebec.

Potentilla monspeliensis L.

P. norvegica var. *genuina* T. H. Wolf.

H.Man. (E. Beckett, 1953); Gillett (20).

Collected from a sheltered crevice on the rocky ridge at Cape Merry, this species is rare at Churchill.

American, boreal; Alaska and California to Labrador, Newfoundland, and South Carolina.

Argentina pacifica Rydb.

Potentilla Egedii Wormskj. var. *groenlandica* (Tratt.) Polunin

H.R. *595.*

This species is not common in our area; it grows along the sandy shore in wet gravelly sand.

American (subarctic) boreal; Alaska and California to Labrador, Newfoundland, and New York.

Dryas integrifolia Vahl.

H.R. *405, 622*; Tyrrell (66), Johansen (31), Gardner (19), Gillett (20).

One of the most widespread and abundant species in the area, it forms a closed mat on exposed gravel and rock ridges, associated with lichens and mosses; it is common in crevices and ledges on the outcrop ridges, and it grows on exposed humus in clearings in the spruce scrub of the ridges. On the stable dunes it forms extensive carpets, associated with *Arctous* and various lichens and mosses.

American, arctic montane; Alaska, British Columbia, and Montana to Northern Labrador and New Hampshire. Here it is near its southern limit for the plains.

Geum perincisum (Rydb.) Raup

G. macrophyllum Willd. var. *perincisum* (Rydb.) Raup

H. Beckett (1954); Gillett (20).

Found in the rich mineral soil of a sheltered gully on the Cape Merry ridge (Mrs. Beckett).

American, boreal; Yukon and California to west coast of Hudson Bay and the Great Lakes region.

Rubus chamaemorus L.

H.R. *452*; Tyrrell (66), Gardner (19), Grøntved (21), Gillett (20).

Common in our area, this is a plant of wet, humous substrata; the underground rhizomes are always found in organic soil. It is common in the spruce woods of the peat plains, usually growing in dense mats of *Cladonia alpestris*; it also grows on the rocky ridge where it is found in open spruce scrub in damp, mossy sites.

Circumpolar, subarctic montane; Alaska and British Columbia to Northern Labrador and New York; throughout the southern part of the Eastern Arctic.

Rubus acaulis Michx.

H.R. *412*; Gillett (20).

Locally common, this plant is found in two habitat types; in the damp humous soil of the ridge spruce scrub, and, more commonly, on the flat, wet sand of the dune 'slacks', usually associated with a willow scrub vegetation.

American, boreal montane; Alaska and British Columbia to Labrador and Gaspé; here it is near its northern limit for the plains region.

Astragalus eucosmus Robinson

H.R. *440*; Grφntved (21), Gillett (20).

This species occurs commonly in dry, sheltered sites, both on the rocky ridge and in stable dunes near the sea.

American, subarctic; Alaska and Colorado to Baffin, Newfoundland, and Maine. Here it is near its southern limit for the plains.

Astragalus alpinus L.

H.R. *413, 502*; Gardner (19), Grφntved (21), Gillett (20).

This is one of the commonest herbs on the dry, exposed summits of both the quartzite and gravel ridges; often it assumes local abundance. It was also observed in the stable dune-heath vegetation of the beaches.

Circumpolar, arctic montane; Alaska and Colorado to Northern Labrador and Newfoundland; occurs in the southern regions of the Eastern Arctic.

Oxytropis campestris (L.) DC. var. *varians* (Rydb.) Barneby

H.R. *422, 497A*; Tyrrell (66), Johansen (31), Grφntved (21), Gillett (20).

Common in the area, it grows on the damp humous soil over gravel on the rocky ridge, and, more commonly on the stable dune-'heath' of coastal sands.

American (the variety) subarctic; confined to the northwest of the continent it is at its eastern limit here.

Oxytropis johannensis (Fern.) Fern.

O. campestris (L.) DC. var. *johannensis* Fern.

H.Man. (E. Beckett, 1953).

The first and apparently the only record from our area, this species was found on the dry, heathy vegetation of the rocky ridge.

American, boreal; Western Hudson Bay to Newfoundland, Gaspé, and Maine. Apparently this is the westernmost locality.

Hedysarum mackenziei Richards.

H.R. *442*; Tyrrell (66), Johansen (31), Gardner (19), Grφntved (21), Gillett (20).

This plant assumes local abundance in dry, heathy sites, growing on the shallow humous soils of the rocky ridge over calcareous gravel and clay, on the stable sands of the coastal vegetation, and on the heathy summits of gravel ridges.

Circumpolar, subarctic montane; Alaska and British Columbia, in the Northwestern Canadian Arctic, to Newfoundland, and Anticosti.

Linum lepagei Boivin

H.R. *462*.

Not uncommon in the area, this plant is restricted to sand and gravel soils. It grows in the dry, unstable dunes along the shore, usually concomitant with *Lesquerella*; it also occurs on dry, calcareous gravel ridges.

American, subarctic/temperate montane; Alaska and Hudson Bay.

Callitriche hermaphroditica L.

(*C. autumnalis* L.)

H.Man. (E. Beckett 1950).

Apparently the only record of this plant from Churchill, it was found in a shallow peaty pool on the summit of the rocky ridge of Cape Merry.

Circumpolar, boreal; Alaska and California to Labrador, Quebec, and New York; here near its northern limit for the plains area.

Viola palustris L.

H.R. *571.*

Rare in the area, the only locality recorded by the present author was at Farnworth Lake where it was growing in the wet marginal community with *Equisetum fluviatile* and *Menyanthes trifoliata.*

Circumpolar, boreal montane; Alaska and Colorado (mountains) to Labrador, Newfoundland, and New Hampshire (mountains). At its northern limit for the plains region.

(*Viola labradorica* Schrank. has been collected just south of our area, by Hughes; H. DAO).

Shepherdia canadensis (L.) Nutt.

H.R. *437*, *638*; Güssow (22), Gardner (21), Gillett (20).

Not uncommon in the region, this shrub grows on dry rocky slopes of the quartzite ridge, in the flat dune 'slack' area, and on the dry, sunny slopes of well-drained gravel ridges.

American, boreal; Alaska, Oregon, and New Mexico (mountains) to Labrador, Maine, and New York; here its northern limit for the central plains.

Epilobium davuricum Fisch.

H.R. *524.*

Not common in the area, it appears to be confined to damp, humus-filled ledges and hollows in the rocky ridges.

Circumpolar, subarctic; Alaska and British Columbia to Labrador and Southern Quebec; throughout the southern part of the Canadian Arctic.

Epilobium palustre L.

H.R. *513*; Gillett (20).

One of the most widespread species in the area, never reaching local abundance, it grows in peaty areas of impeded drainage—in the sedge bogs, the wet dune 'slacks', and in damp humus of crevices and hollows on the rocky ridge.

Circumpolar, boreal montane; Alaska and Colorado (mountains) to Labrador and Newfoundland. Near its northern limit for the central plains.

Epilobium glandulosum Lehm. var. *adenocaulon* (Haussk.) Fern.

E. adenocaulon Haussk.

H. Beckett (1954).

Not common, it occurs in damp, marshy sites on the lower flanks of the rocky ridge near the township of Churchill.

American, boreal; Alaska and New Mexico to Northern Quebec, Newfoundland, and Pennsylvania.

Chamaenerion angustifolium (L.) Scop.

Epilobium angustifolium L.

H.R. *609*; Gardner, (19), Grφntved (21), Gillett (20).

A common plant in the area, it appears to be indigenous in most habitats. It is common on the dry stable dunes extending on to the humous soil of ledges and sheltered niches on the rocky ridges.

Circumpolar, boreal reaching the subarctic; Alaska and New Mexico to Baffin, Labrador, and North Carolina.

Chamaenerion latifolium (L.) Sweet.

Epilobium latifolium L.

H.R. *608*; Grφntved (21), Gillett (20).

This elegant plant is most common on the stable sandy shores of our area where it forms very local pure stands. It also occurs, less commonly, on dry sheltered ledges on the Cape Merry Ridge.

Circumpolar (incompletely), arctic montane; Alaska and Colorado, throughout the Canadian Arctic to Labrador, Newfoundland, and Gaspé.

Myriophyllum exalbescens Fern.

H.R. *480*; Gillett (20).

Apparently not a common plant here it was observed in a few peaty pools on the rocky ridge of Cape Merry, between Fort Churchill and the Churchill township; in such habitats it forms a dominant zone near the periphery of the pools, rooted in submerged peat.

American, boreal; Alaska and New Mexico to Labrador, Newfoundland, and New Jersey.

Hippuris vulgaris L.

H.R. *457*, *490*; Johansen (31), Gardner (19), Grønntved (21), Gillett (20).

Common in the area, it is found in ponds and lakes over mineral soil—gravelly mud and silt; it also grows in the peaty soils of tarns in the plains, forming a discrete zone in the marginal vegetation.

Circumpolar, subarctic/boreal; Alaska and New Mexico (mountains) to Labrador and New York.

Hippuris tetraphylla L. f.

(*H. vulgaris* L. var. *maritima* Hartm.)

H.R. *600*; Gillett (20).

As generally, this plant is confined to maritime habitats; it grows in wet, sandy flats along the shores, forming local facies by means of its close rhizomatous branching.

Circumpolar, boreal maritime; Alaska, coastal to Northern Labrador and Gaspé.

Cicuta mackenzieana Raup

H.Man. (Beckett, 1953); Johansen (31), Grønntved (21), Gillett (20).

This plant is most common in the marginal vegetation of shallow pools on the rocky ridge.

American, subarctic/boreal; Alaska and the Northwest Territories, here at its eastern limit.

Moneses uniflora (L.) Gray

H.R. *416*, *574*; Gillett (20).

Fairly widespread, but never common, this species is confined to the shaded, mossy substrata of spruce woods, both on the ridges and in the plains.

Circumpolar, boreal; Alaska and Colorado to Labrador and Pennsylvania; near its northern limit here, for the plains region.

Pyrola grandiflora Radius.

H.R. *495*; Gardner (19), Grønntved (21), Gillett (20).

Not uncommon in the area, it grows in humous soil of ledges in the quartzite boulders of the ridges, extending into sheltered hollows where it often grows with *Salix reticulata* and *Vaccinium uliginosum*.

Circumpolar, arctic/subarctic; Alaska and British Columbia throughout the southern Canadian Arctic to Labrador and Gaspé.

Pyrola minor L.

H. Beckett (1954); Gillett (20).

Not at all common in the area, this plant was recorded in the damp, shaded organic soil of the spruce wood near Farnworth Lake (Mrs. Beckett).

Circumpolar, boreal; Alaska and New Mexico to Labrador and New England; here at its northern limit for the plains.

Ramischia secunda (L.) Garcke.

Pyrola secunda L.

H.R. *623*; Gillett (20).

Not common, this plant grows in sheltered ledges and crevices on the rocky ridge, often accompanied by *Cystopteris fragilis* and *Minuartia rubella*.

Circumpolar, boreal; Alaska and New Mexico to Northern Labrador and Maryland.

Ledum groenlandicum Oeder.

H.R. *443*; Gardner (19), Grønntved (21), Gillett (20).

One of the dominants of the spruce forest ground flora, it grows on peat hummocks and ridges, forming pure stands locally; it is most abundant where the wet peat is slightly drained.

American, boreal; Alaska and Washington to Northern Labrador and New Jersey; here it is near its northern limit for the plains.

Ledum decumbens (Ait.) Lodd.

L. palustre L. var. *decumbens* Ait.

H.R. *406*; Güssow (22), Johansen (31), Gardner (19), Grønntved (21), Gillett (20).

This prostrate, dwarf shrub reaches its greatest abundance on the damp, exposed heaths of the rocky ridge where it is often concomitant with *Dryas*, *Vaccinium vitis-idaea*, and *Loiseleuria procumbens*.

Circumpolar, low-arctic; Alaska and throughout the Southern Arctic to Northern Labrador and Quebec.

Rhododendron lapponicum (L.) Wahl.

H.R. *441*; Tyrrell (66), Güssow (22), Johansen (31), Gardner (19), Grφntved (21), Gillett (20).

Common in the area, this small shrub is found in damp, humous substrata; it occurs in the spruce scrub on the rocky ridges and is occasional in the *Dryas*-dominated community on the stable dunes; it forms local facies on the summits of hummocks in the peat bogs of the plains area.

Circumpolar, arctic (subarctic) montane; Alaska and British Columbia, throughout the southern part of the Canadian Arctic, to Labrador and New England (mountains).

Loiseleuria procumbens (L.) Desv.

H.R. *484, 538*; Gillett (20).

Of local occurrence, this prostrate shrub forms dense mats on the exposed, dry humus on the quartzite ridges; its most frequent associates are *Empetrum nigrum* and *Vaccinium uliginosum*.

Circumpolar, subarctic montane; Alaska and Alberta to Labrador, Newfoundland, and New Hampshire; common in the southern regions of the Canadian Arctic.

Kalmia latifolia L.

H.R. *565*; Gillett (20).

This plant is not common in our area; it grows in damp peat in sheltered localities; the present author's specimens came from a *Sphagnum* hummock in the spruce wood near Farnworth Lake.

American, boreal; Alaska and California to Labrador and Pennsylvania; near its northern limit for the plains.

Andromeda polifolia L.

H.R. *401, 424*; Tyrrell (66), Johansen (31), Grφntved (21), Gillett (20).

A common plant here, this dwarf shrub is found in damp humous substrata on the outcrop areas, both in open habitats and in the spruce scrub; it also grows in well-drained peat in the spruce woods of the plains.

Circumpolar, boreal; Alaska and Idaho to Northern Labrador and Southern Manitoba; replaced eastwards by *A. glaucophylla* Link., the western limit of which appears to be Southeastern Hudson Bay and Eastern Manitoba.

Arctostaphylos uva-ursi (L.) Spreng var. *coactilis* Fern. and Macbr.

H.DRNL.; Gillett (20).

Although a collection was not made, the present author recorded this plant at Twin Lake Hill where it grew on dry, gravel slopes, associated with *Shepherdia* and *Juniperus communis*. It appears to be rare in our region, being confined to sand and gravel deposits.

Circumpolar, boreal (the species); the variety, from Yukon and Colorado to Newfoundland and Virginia.

Arctous alpina (L.) Niedenzu

Arctostaphylos alpina (L.) Spreng.

H.R. *613*; Tyrrell (66), Johansen (31), Gardner (19), Grφntved (21), Gillett (20).

At Churchill it is possible to distinguish this species from *A. rubra* only when ripe fruits are available; the distinguishing vegetative characters which Fernald (18) describes were found to be unreliable with much of the material. Also the apparent ecological differences between the two, clear in other areas, are not readily detectable here. Hultén (26) and Polunin (42) have suggested that there is evidence for hybridization in this region, and this seems a reasonable hypothesis. In general *A. alpina* is confined to dry, exposed heaths on the ridges, growing on the shallow humus over bare rock.

Circumpolar, subarctic/arctic montane; Alaska and British Columbia to Northern Labrador and New England; through the Southern Canadian Arctic.

Arctous rubra (Rehd. and Wils.) Nakai

Arctostaphylos rubra (Rehd. and Wils.) Fern.

H.R. *464*; Gillett (20).

This plant is most common on the dry, calcareous dunes adjacent to the rocky ridges on Cape Merry; in this habitat it occurs as a co-dominant with *Dryas*, and it forms widespread

mats of rhizomes in the upper humous horizons of the soil. It also extends on to the ridges where it appears to be closely concomitant with the previous species, but the difficulties of identification prohibit a comprehensive study of their autecology.

Circumpolar, subarctic; Alaska and British Columbia to Newfoundland and Southeastern Quebec.

Vaccinium uliginosum L.

H.R. *415*; Tyrrell (66), Johansen (31), Gardner (19), Grøntved (21), Gillett (20).

This shrub is common in the area, being found in sheltered sites on the quartzite ridges, usually on ledges or against rock facies, rooted in damp humus. Of the limited material which the present author has seen from this area, none could be satisfactorily identified with the northern *V. microphyllum* (Lange) Hagerup, although there is considerable variation in vegetative characters.

Circumpolar, boreal montane; Alaska and British Columbia to Northern Quebec, Newfoundland, and New Hampshire (mountains).

Vaccinium vitis-idaea L. ssp. *minus* (Lodd.) Hult.

V. vitis-idaea L. var. *minor* Lodd.

H.R. *402*, *491*; Tyrrell (66), Güssow (22), Johansen (31), Grøntved (21), Gillett (20).

Locally abundant on the exposed heaths, it is most common in humus-filled rock crevices and on angled rock surfaces on which it forms a dense mat with various lichen species.

The whole species circumpolar, boreal montane; the subspecies, subarctic/boreal montane; Alaska and British Columbia to Quebec and Vermont; extending into the Southern Arctic.

Oxycoccus microcarpus Turcz.

Vaccinium oxycoccus of American authors.

H.R. *516*; Johansen (31), Gardner (19), Gillett (20).

Not common in the area, and never locally abundant, it is found in eutrophic peat bogs, associated with sedges, *Sphagnum* species, and various hypnaceous mosses.

Circumpolar, boreal montane; its imperfectly known American distribution would appear to be from Alaska and British Columbia (mountains) to Northern Labrador and Gaspé.

Empetrum hermaphroditum (Lange) Hagerup

H.R. *487*; Güssow (22), Johansen (31), Gardner (19), Grøntved (21) var. *hermaphroditum* (Lange) Sørensen, Gillett (20).

A common plant of the dry, heathy vegetation on the ridges, it co-dominates locally with other prostrate shrubs and *Dryas*. It also grows in the dry, stable sand dune community, and on the thin humous soil of gravel ridge summits.

Circumpolar, boreal; Alaska to Labrador and Newfoundland.

Primula stricta Hornem.

H.R. *478*; Johansen (31), Gardner (19), Gillett (20).

In the area, it is confined to sheltered habitats of damp, eutrophic conditions of substratum. It is common in the dune 'slack' areas on the seaward side of the ridges, extending into willow scrub on the damp, stable dunes.

Circumpolar, subarctic; Alaska and Mackenzie to Labrador and Western Quebec; southern limits at Great Slave Lake and James Bay.

Primula egaliksensis Wormskj.

H.R. *479*, *517*; Gardner (19), Gillett (20).

With similar ecological amplitude to the previous species, this plant is often found in close association with it, particularly in wet dune areas and in coastal willow scrub. It is also locally common in eutrophic bogs flanking inland gravel ridges, where it is associated with various herbs and sedges of base-rich affinities.

American, subarctic; Alaska and British Columbia to James Bay, Newfoundland, and Quebec.

Androsace septentrionalis L.

H.R. *496*; Tyrrell (66), Güssow (22), Johansen (31), Gardner (19), Gillett (20).

Locally common on exposed, frequently disturbed sand dunes, it is often concomitant with *Lesquerella arctica*. It is confined to dry sand and gravel habitats.

Circumpolar, boreal and arctic, montane; Alaska and California (to New Mexico) to Labrador, Newfoundland, and Gaspé; scattered in the Canadian Arctic.

Gentianella propinqua (Richards.) Sm.

Gentiana propinqua Richards.
H.R. *610*; Grφntved (21), Gillett (20).
A common species on the dry, open dunes of the coastal areas, it grows in local abundance in the *Elymus*—dominated zone.
American, subarctic montane; Alaska and Southern British Columbia to Newfoundland and Gaspé.

Lomatogonium rotatum (L.) Fries.

Pleurogyne rotata (L.) Griseb.
H.DRNL.; Johansen (31), Gardner (19), Gillett (20).
At Churchill it is common along the margins of parts of the 'townsite slough', and it occurs in the mud-flat communities of the river estuary (Mrs. Beckett).
Circumpolar, boreal; Alaska and British Columbia to Labrador, Newfoundland, and Gaspé.

Menyanthes trifoliata L.

H.R. *528*; Gillett (20).
Common in areas of poor drainage, it appears to be confined to the margins of shallow pools and tarns; it grows in the submerged peat.
Circumpolar, boreal; Alaska and Colorado to Labrador, Newfoundland, and Virginia.

Mertensia maritima (L.) S. F. Gray var. *tenella* Fries.

H.Man. (E. Beckett); Johansen (31), Gardner (19).
This plant was recorded on a gravelly beach in the foreshore vegetation at Cape Merry (Beckett).
Circumpolar, arctic–subarctic; Alaska and British Columbia to Northern Labrador, Newfoundland, and Connecticut; throughout the Canadian Arctic.

Limosella aquatica L.

H.NM. *96860* (Porsild, 1930).
The specimen cited was collected from "small very shallow pools that remain throughout the summer" on the rocky ridge.
Circumpolar, boreal-temperate; British Columbia to Labrador and Newfoundland. Here at its northern limit for the plains See Porsild (46, p. 62).

Euphrasia frigida Pugsl.

E. arctica auct. non Lange
H.Man. (E. Beckett, 1950); Gillett (20).
It occurs occasionally on exposed ridges in damp, humous soil, and it was noted in the dry, stable dune-heath vegetation near Fort Churchill.
Amphi-Atlantic, arctic montane; Keewatin and Western Hudson Bay to Baffin, Northern Labrador, Quebec, and Gaspé; south to the Great Lakes area.

Castilleja pallida L. ssp. *elegans* (Malte) Pennell

H.Man. (Buller, 1939); Johansen (31), Grφntved (21), Gillett (20).
Gillett records this along wet stream banks, with apparently base-rich soil tendencies. All the present author's material was of the following species.
American, arctic–subarctic; Alaska to Hudson Bay, here at its eastern limit.

Castilleja raupii Pennell

H.R. *423*; Gillett (20).
A common plant in the area, usually found on damp peat over gravel and clay, often forming small colonies; it also extends in to the dry, stable dunes where it is concomitant with *Elymus* and *Arctous rubra*.
American, subarctic; Yukon and Northern Alberta to Western Hudson Bay and James Bay.

Bartsia alpina L.

H.R. *446*; Tyrrell (66), Gardner (19), Grφntved (21), Gillett (20).
Of local occurrence, it is confined to the damp, mossy humus of open patches in the spruce scrub on the outcrop ridges, usually concomitant with *Geocaulon lividum* and *Cypripedium passerinum*.
Amphi-Atlantic, arctic montane; Western Hudson Bay, South Baffin, Northern Quebec, and Labrador; here at its western limit in America.

Rhinanthus borealis (Sterneck) Marshall

R. groenlandicus Chabert var. *Drummond-Hayii* (B. White) Ostenf.
H.R. *611*; Gillett (20).
This plant is never abundant and only of local occurrence, growing chiefly in the dry dune-grassland community of the sand deposits, in the *Elymus* zone.
American (Iceland), subarctic montane; Alaska and Mackenzie to Northern Labrador, Gaspé, and New York; extends into Western Europe and Eastern Asia.

Pedicularis flammea L.

H.R. *509*; Gillett (20).
This plant is local in occurrence, being found in eutrophic marshes and tarns in the plains area, usually occurring in small colonies.
Circumpolar, arctic montane; Yukon and British Columbia (mountains) to Northern Labrador and Gaspé; throughout the Southern Canadian Arctic.

Pedicularis groenlandica Retz.

H. Beckett (Coll. 1950).
Of this species Mrs. Beckett writes (private communication):"it is common in wet open glades in the woods just south of the town". This is the only record.
American, arctic; Northwest Territories and New Mexico (mountains) to Northern and Southeast Labrador.

Pedicularis labradorica Wirsing

H.R. *492*; Grøntved (21), Gillett (20).
Not common, it is found only on the dry, exposed outcrop ridges where it grows on damp mats of humus over boulders, usually associated with *Dryas integrifolia* and lichens.
Circumpolar (incompletely), boreal/subarctic; Alaska and British Columbia to South Baffin, Northern Labrador, and James Bay.

Pedicularis lapponica L.

H.R. *414*; Tyrrell (66), Gardner (19), Grøntved (21), Gillett (20).
Not uncommon on dry, humous substrata, it is frequent in open sites in the spruce scrub on the ridge, occurring with *Platanthera hyperborea* and *Orchis rotundifolia*.

Pedicularis sudetica Willd.

H.R. *498*, *510*; Grøntved (21), Gillett (20).
It is found most frequently on thin, wet humus or peat over calcareous, clayey gravel, often associated with *Castilleja raupii* and various sedges. It grows on deeper eutrophic peats of the bog areas.
Circumpolar, arctic montane; Alaska and Northern British Columbia, throughout the Canadian Arctic to North Baffin and James Bay.

Pinguicula vulgaris L.

H.R. *403*; Tyrrell (66), Gardner (19), Grøntved (21), Gillett (20).
A common plant of our region, it is found on damp peat of the open heath on outcrop and gravel ridges, extending into peat hummocks in the sedge-bog vegetation.
Circumpolar, boreal; Alaska and Washington to Labrador, Gaspé, and Vermont, largely confined to the boreal forest zone with a locality in South Baffin.

Pinguicula villosa L.

H.DAO. *2071*; Gillett (20).
"In a Sphagnum bog; W. side of the river at Hudson Bay Co. Post" Gillett (annotation on *exsiccatum*).
Circumpolar, subarctic montane; Alaska and Mackenzie to Northern Labrador and Eastern Hudson Bay.

Utricularia vulgaris L.

H.DRNL.; Gillett (20).
Of local occurrence, it grows in the wet marl and mud of the river flats, forming local colonies of considerable density.
Circumpolar, boreal; Alaska and New Mexico to Southern Labrador, Newfoundland, and Florida.

Utricularia intermedia Hayne.

H.R. *591*; Gillett (20).

Not widespread, it is locally abundant in peaty flats over clayey gravel, partially submerged in spring and drying out in summer; in such situations it flowers profusely. It is commonly concomitant with *Eriophorum angustifolium*.

Circumpolar, boreal; Alaska and Southern British Columbia to Southern Labrador and New Jersey.

Utricularia minor L.

H.DRNL.; Gillett (20).

Gillett records this species from similar habitats to those of the previous species; it appears that it is less common in the area.

Circumpolar, boreal; Yukon and Colorado to Southern Labrador, Newfoundland, and Connecticut.

Plantago maritima L. ssp. *juncoides* (Lam.) Hultén

P. maritima var. *glauca* Hornem.

H.R. *599*; Johansen (31), Gillett (20).

It occurs along the shores, growing in wet sand and gravel; it is a plant of the halophytic, foreshore vegetation.

Incompletely circumpolar, subarctic; Alaska to Hudson Bay.

Galium trifidum L.

H.DAO. *2202*; Gillett (20).

Gillett's annotation indicates that this is scarce, his specimen coming from the "marshy border of Farnworth Lake".

Circumpolar, boreal; Alaska and Colorado to Southern Labrador, Newfoundland, and New England.

Galium brandegei Gray

H.R. *572*.

The only collection was made at Farnworth Lake where it was growing with *Comarum palustre*, *Equisetum fluviatile* and, rarely, *Viola palustris*.

American, (Iceland), boreal; Alaska and New Mexico to Labrador, Gaspé, and Maine; here near its northern limit for the central plains.

Linnaea borealis L. ssp. *americana* (Rehd.) Hultén

H.NM. (Porsild, July 1930).

Porsild collected this species at Mosquito Point, on the west side of the Churchill River, seven miles from the mouth.

American, boreal; Alaska and Southern British Columbia to Northern Quebec and Labrador, Newfoundland, and New Jersey.

Campanula uniflora L.

H. Man. (E. Beckett 1950).

The only known station in our area is at Sloop's Cove on the west side of the Churchill River, where the plant grows in humous substrata of sheltered rocky ledges and crevices.

Circumpolar, arctic montane; Alaska and Colorado (mountains) throughout the Canadian Arctic to Labrador, Newfoundland, and Gaspé. Here it is near its southern limit for the plains.

Campanula uliginosa Rydb.

H. Beckett (1954).

Apparently the first collection from our area, this plant was found by Mrs Beckett in the wet, clayey soil of the large slough in Churchill townsite.

American, boreal; Saskatchewan and Nebraska to Southern Quebec and Massachusetts.

Solidago multiradiata Ait.

H.R. *604*; Grønvet (21), Gillett (20).

Common throughout the area, it is usually found on dry ledges of the outcrops and on the dry, sandy gravel of the coastal dunes and the inland gravel ridges.

American, subarctic/boreal montane; Alaska and British Columbia to South Baffin, Labrador, and Gaspé.

Erigeron elatus Greene

H.R. *541*; Gillett (20).

Not common in the area, it is found on the summits of gravel ridges on dry, often calcareous substrata.

American, boreal; Alaska and British Columbia to Newfoundland and Gaspé.

Erigeron humilis Graham

E. unalaschkensis (DC.) Vierh.

H.R. *619*.

The only locality for this plant was on the sand dune area near Fort Churchill where it was growing in damp sand at the margin of one of the dune hollows or flushes. This record appears to be the first for Manitoba.

Circumpolar, arctic montane; Alaska, British Columbia, and Montana, throughout the Southern Arctic to Labrador and James Bay. Here it is at its southern limit for the central plains.

Erigeron angulosus Gaudin var. *kamtschaticus* (DC.) Hara.

H.DRNL.; Gillett (20).

This plant is infrequent on dry gravel ridges.

Circumpolar, boreal; Alaska and Colorado to Southern Labrador, Gaspé, and Maine.

Achillea millefolium L. var. *nigrescens* Meyer

H. Man. (Beckett 1950); Tyrrell (66), Johansen (31), Gardner (19), Gillett (20).

A common plant on dry, grassy slopes throughout the area.

Circumpolar, boreal; Alaska and Colorado to Labrador, Newfoundland, and New Hampshire.

Achillea borealis Bong.

(I prefer to leave this as a separate species rather than follow Boivin (12) who includes this and the preceding as different varieties of *A. millefolium* L. ssp. *atrotegula* Boivin. This species is readily distinguished from *A. millefolium* L. by its slender habit, and round-topped corymb with black margins to the phyllaries.)

H.R. *435*; Gillett (20).

Infrequent in the area, it is found on the stable, damp sands of the upper beach zones and in the 'dune-slack' communities. It also occurs on damp, humous soil over gravel on the rocky ridge.

American, subarctic/boreal montane; Alaska and New Mexico to Labrador, Newfoundland, and New Hampshire.

Tripleurospermum ambiguum (Ledeb.) Löve and Löve

Matricaria ambigua (Ledeb.) Kryl.

H.R. *605*; Gillett (20).

This is common on the foreshore gravel of the coastal beaches.

Circumpolar (incompletely) subarctic; Alaska to Northern Labrador.

Chrysanthemum arcticum L.

H.R. *606*; Güssow (22), Johansen (31), Gillett (20).

Confined to the shore line, it occurs in the halophytic vegetation on sand and gravel flats near high tide level; usually concomitant with *Tripleurospermum ambiguum* and *Honkenya peploides*.

Incompletely circumpolar, subarctic maritime; Alaska to Northern Labrador and Southern Hudson Bay.

Petasites sagittatus (Pursh.) Gray

H.R. *513*; Grøntved (21), Gillett (20).

Not common in the area, the author's specimen was from an eutrophic bog flanking an inland gravel ridge at Christmas Lake in the northeastern corner of the area. The only other locality noted was on the northwestern side of Farnworth Lake in a similar habitat.

American, boreal/subarctic; Alaska and Colorado to Labrador, James Bay, and Southern Quebec.

Petasites palmatus (Ait.) Gray

H. Beckett (1954); Gillett (20).

This plant has been recorded from wet, marshy meadows near Warkworth Creek, in the southwestern corner of our area.

American, boreal; Alaska and Yukon to Northern Labrador, Newfoundland, and Massachusetts.

Arnica alpina (L.) Olin ssp. *attenuata* (Greene) Maguire

Arnica attenuata Greene
H.R. *467*; Tyrrell (66), Johansen (31), Gardner (19), Gillett (20).
Locally abundant, it occurs in damp soil in ledges, hollows, and crevices on the outcrop ridges.
This subspecies occupies the western and southern part of the range of the whole species in North America: from Alaska and Alberta to the West Coast of Hudson Bay. Here at its western limit.

Senecio pauperculus Michx.

H. Man. (E. Beckett, 1950); Gardner (19), Grøntved (21), Gillett (20).
A common species in the area, growing in wet, calcareous gravels along the shore and on inland gravel ridges, extending into shallow peat bogs over till.
American, boreal montane; Alaska and Southwestern British Columbia to Ungava, Newfoundland, and Maine.

Senecio congestus (R. Br.) DC. var. *palustris* (L.) Fern.

Senecio palustris (L.) Hook.
H.R. *546*; Tyrrell (66), Johansen (31), Grøntved (21), Gillett (20).
A locally common species, it grows in open marshy sites, often rooted in shallow, submerged peat at pond margins, generally forming small colonies.
Circumpolar (incompletely) subarctic; Alaska to Labrador, Southern Quebec, and Iowa.

Senecio indecorus Greene

H.NM. *110668* (Porsild, 1930).
American, boreal; Yukon and Idaho to Gaspé and the Great Lakes.

Taraxacum lacerum Greene

T. groenlandicum Dahlst.
H.Man. (E. Beckett, 1953).
Common on the dry, humous soil of the outcrop ridge, particularly around habitations, was noted in many localities where open conditions of habitat prevailed.
American, arctic; Alaska and British Columbia to East Baffin, Newfoundland, and Gaspé.
There is at least one other distinct species within the *ceratophorum* complex at Churchill; this will be described when more material is available; previously it has been identified with the collective *Taraxacum ceratophorum*.

V. The Geographical Affinities of the Flora

The following treatment of the flora attempts no more than to assign the 270 species of the Churchill region to certain broad geographical groupings; it is hoped that the flora of the region of Western Hudson Bay as a whole will be studied in phytogeographical detail at a later date—such a treatment is beyond the scope of this account.

Considering the latitudinal affinities, four groups have been distinguished. The first (1) consists of the *cosmopolitan* or wide-ranging species of which there are four at Churchill—*Equisetum arvense, Cystopteris fragilis, Carex aquatilis*, and *Lemna trisulca*. The second (2) is made up of *arctic* species, consisting of 78 entities which are, for the most part, wide-ranging, often montane, being confined in Central North America to the true Arctic. In many instances the southern limit of the areas of these species lies at Churchill (considering the central plains region), though many extend along the arctic fringe of Hudson Bay to James Bay (55°N.) and others have small disjunct areas in the Great Lakes area.

The largest group in this classification numbers 122 entities and comprises the *boreal* element of the flora (3). With few exceptions these plants occur only

south of the tree line in North America, and a considerable proportion is montane both in the east and the west. Churchill lies on the tree line and these species are at, or near, their northern limits for the plains region. The fourth group (4) is less easily defined and is described here as that group of species which evince *subarctic* affinities. It consists of plants whose areas lie along the tree line, extending for varying distances to the north and south. *Betula glandulosa* (mapped in Raup (53)) exemplifies this group well; it is low-arctic in the north, most abundant in the hemi-arctic zone (Rousseau (59)), but extends southwards into the northern or subarctic zones of the coniferous forest, occurring in open situations at lake margins. In general they are plants of open or incompletely shaded habitats, and the following species are typical examples of the 66 entities which make up the group: *Tofieldia pusilla*, *Anemone parviflora*, *Coptidium lapponicum*, *Parnassia kotzebuei*, and *Andromeda polifolia*. These groupings have been summarized in Table II.

TABLE II

Latitudinal affinity	No. of species	% of total
(1) Cosmopolitan species	4	1.50
(2) Species whose areas are arctic or arctic-montane in North America	81	28.80
(3) Boreal species, at or near their northern limits in the central plains	122	45.20
(4) Species whose areas coincide with the hemi- and subarctic zones	66	24.40

The affinities of the flora can be studied further by arranging the species according to the lateral disposition of their areas in the Northern Hemisphere. The largest group (*a*) consists of species whose areas are more or less continuous round the Northern Hemisphere—the *circumpolar* species which at Churchill amount to 147. A related group (*b*) is made up of those circumpolar entities which are rare and *isolated in Northwestern Europe and absent in Asia* (cf. Hultén (27, p. 46) and Raymond (54, p. 17)). At Churchill this group is represented by nine species—*Carex scirpoidea*, *Stellaria humifusa*, *Stellaria calycantha*, *Draba crassifolia*, *Potentilla pulchella*, *Primula stricta*, *Rhinanthus borealis*, *Pedicularis flammea*, and *Campanula uniflora*.

Group (*c*) consists of those species which occur on both sides of the Atlantic but are absent from Western America, Asia, and Eastern Europe—the *amphi-Atlantic* species. It is represented at Churchill by the following species:

Carex adelostoma
Spiranthes romanzoffiana
Draba incana
Euphrasia frigida
Bartsia alpina
Saxifraga aizoides

On an areal basis, one can readily distinguish three groups within the American species at Churchill. The largest is that of the wide-ranging or *transcontinental* species, group (*d*), the 81 members of which have continuous areas across the continent, many of the arctic and subarctic members occurring also in Greenland. North American species whose main areas lie in *Western*

North America and whose eastern limits are in this region (Western Hudson Bay) comprise 6.30% of the flora and consist of the following species, group (*e*):

Cypripedium passerinum
Elymus innovatus
Salix glauca var. *acutifolia*
Salix brachycarpa var. *mexiae*
Salix alaxensis
Salix arbusculoides
Ranunculus purshii (extending east to the St. Lawrence)
Anemone richardsonii (and Greenland, Böcher (8, 9))
Ribes oxyacanthoides
Ribes hudsonianus
Fragaria glauca
Geum perincisum
Oxytropis campestris var. *varians*
Hedysarum mackenziei (extending east to the St. Lawrence)
Cicuta mackenzieana
Gentianella propinqua (disjunct in Newfoundland)
Castilleja pallida ssp. *elegans*
Erigeron elatus (extending east to the Gaspé Peninsula)

The species *Juniperus communis* var. *depressa*, *Pucinellia langeana*, *Draba minganensis*, *Oxytropis johannensis*, *Salix calcicola*, *S. pellita*, comprise the small, strictly eastern element (*f*) of North American entities; their western limits lie in the region of the west coast of Hudson Bay.

This arrangement of the flora can be summarized as in Table III. (This table does not include *Carex oligosperma* var. *churchilliana* and *Melandrium gillettii* which are endemic to the Churchill region).

TABLE III

	No. of species	% of total
(*a*) Circumpolar species	147	54.40
(*b*) Incompletely circumpolar, absent in Asia, isolated in Northwestern Europe	9	3.30
(*c*) Amphi-Atlantic species	6	2.20
(*d*) American transcontinental species	80	30.00
(*e*) Western species near their eastern limits in the Hudson Bay region	18	6.30
(*f*) Eastern species, near their western limits in the Hudson Bay region	8	3.00

Within these broad groupings (Tables II and III) there are many phytogeographical ramifications which can be recognized, but their treatment must await the accumulation of more comprehensive data of distribution and the establishment of intraspecific genetic relationships over the greater part of the areas of individual species.

NOTE: Since the completion of this account it has been pointed out that *Equisetum sciopoides* Michx. and *Carex leptalea* Wahl. should be included in the flora of the area.

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